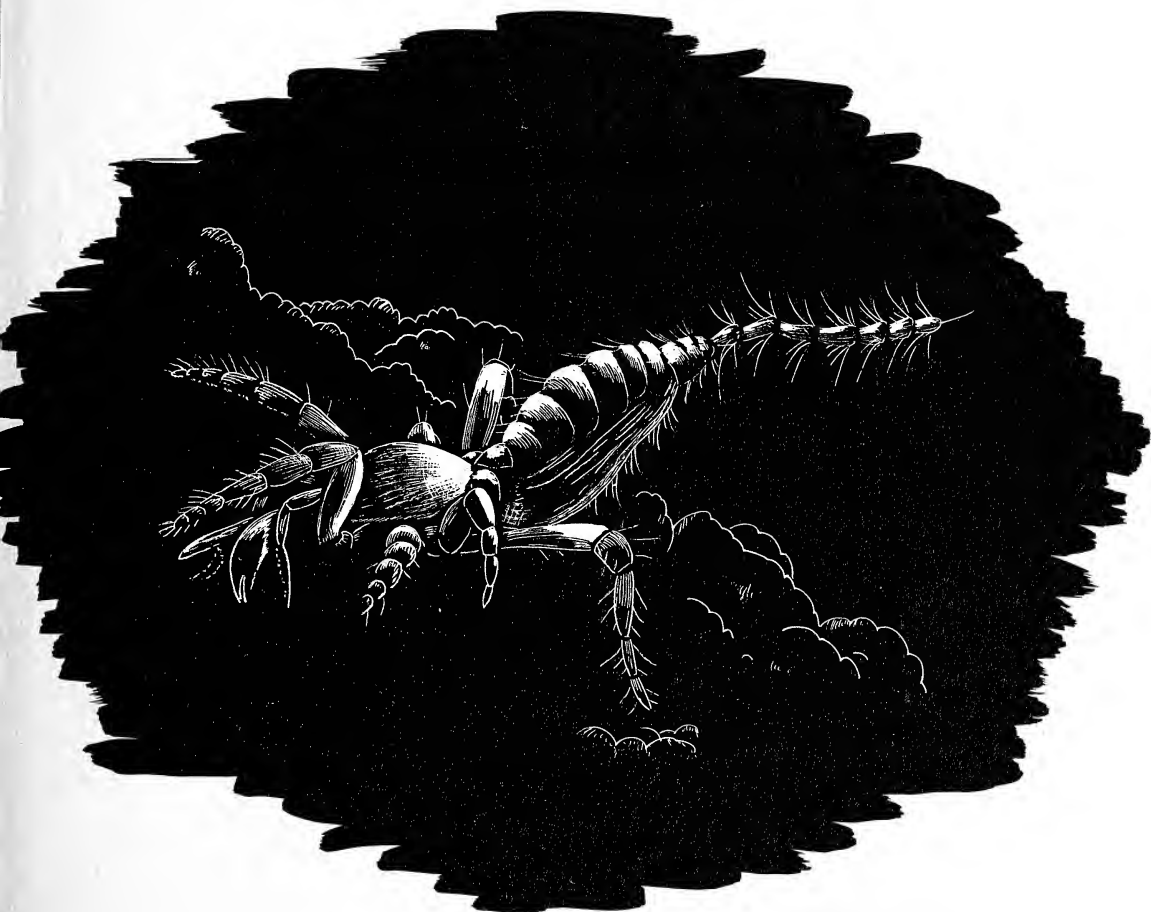


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THE IMPORTANCE OF COMMUNAL EXPERIENCE TO SURVIVAL FOR SPIDERLINGS OF *ARANEUS DIADEMATUS* (ARANEAE: ARANEIDAE)¹

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ABSTRACT

Outdoors, newly hatched *Araneus diadematus* spiderlings collectively inhabit a communal web until the onset of solitary orb-weaving. In the laboratory, isolated eggs hatched more frequently than grouped ones; most animals reared in isolation survived, but their mortality was greater than among communally reared controls. Spatial measurements on the communal web showed significant spreading of animals over time, an effect facilitated by low relative humidity. Animals reared in isolation subsequently built functional orb webs, though there were significant web differences between groups in protein content, size, regularity, and hub location measures. The results suggest that communal life is nonessential for hatching and growth of animals, though maturation is slower in isolates. The communal web period is discussed as flexible time which permits adjustment of ontogenetic development to varying environmental conditions.

INTRODUCTION

Most spiders, despite their diverse ecologies and intrinsic characteristics (approximately 30,000 described species, Levi and Levi 1968), undergo an early development marked by a number of common elements (Gertsch 1949, Bristowe 1939, Turnbull 1973). Among the most striking developmental features are instances of grouping by spiderlings. Soon after hatching, these immature creatures wiggle and clump considerably. They typically molt at least once within the egg sac. Postmolt gregariousness follows. Soon after that the young collectively vacate their hatching site while they carry substantial quantities of abdominal yolk.

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Generally speaking, the young of orb-weavers continue to group after leaving their birth place. Outside the egg sac these spiderlings remain together on a single web for a week or so, presumably until the yolk supply is assimilated (Bristowe 1939). Then this familial group scatters, and individuals pursue, with the exception of mating, solitary lives.

Many descriptions from McCook (1890) to Mayer (1953) support the preceding ontogenetic outline for the cross spider, *Araneus diadematus* Clerck (Levi 1971). This study examines the spatial pattern assumed when first or second instars group; it also tests the survival value of grouping behavior.

Within the laboratory, these spiderlings exhibit gregarious behavior at two periods: while inside the egg sac and after emerging onto threads jointly constructed in the sac's immediate vicinity. During the first period the hatchlings, between bouts of leg flexures and extensions, cling to one another forming pairs or larger clumps of animals. Second instars behave similarly inside the egg sac; they mass tightly into dark clumps consisting of fifty to several hundred spiderlings. Rearing experiments (solitary versus group-reared) provide evidence suggesting that grouping affects viability.

About six and one-half days after hatching, the second instars emerge upwards, laying threads as they move. This collective activity creates a sheet-like, silk structure called the communal web (Figs. 1-6) because it resembles the communal web of social spiders (Shear 1970). The spiderlings cluster peacefully on the web for about three days. Mostly they hang motionless, sometimes they touch one another, and occasionally they carry out particular thread-laying behaviors that recall movements used to weave the orb web (Witt *et al.* 1968). Several days later, coexistence between siblings gives way to aggressiveness; gnats, rejected earlier as prey, are now accepted. Then, under appropriate meteorological conditions, the animals disperse (Platnick 1976) by ballooning (dispersion through the air by means of silk threads), and individuals become solitary orb weavers.

The gregariousness seen on the communal web is examined from two perspectives. First, isolation experiments look into the relevance of communal web experience in the development of solitary web-building behavior. Second, the nature of the spiderlings' spatial arrangement while on their common web, and its variation over time, are analyzed by the nearest neighbor method (Clark and Evans 1954). Also, the hypothesis is tested that humidity significantly influences the spatial arrangement; this conjecture seems attractive because animals with high surface-to-volume ratios usually have problems with water balance (Cloudsley-Thompson 1962).

MATERIALS AND METHODS

Rearing Experiments.—Spiderlings (*Araneus diadematus* Cl.) were reared from egg sacs obtained from Upstate New York (Mr. Leonard Pankhurst, 204 Stroud Street, Canastota, N. Y.). Egg sacs not used immediately were stored in a refrigerator at 7°C for periods of one to two months. An egg mass was prepared for experimentation by removing it from the sac and separating it completely into individual eggs. These eggs were incubated in high ambient humidity (above open water pans) while automatic temperature and light control simulated a 16 hr day and 8 hr night. From January through July, daily maximum temperatures averaged $25.9 \pm 1.7^\circ\text{C}$ (SD); nightly minimums averaged $21.9 \pm 1.3^\circ\text{C}$.

Some of the eggs separated from a given egg mass were raised in isolation; the remainder were reared communally. An egg (chosen at random) was isolated by placing it alone on a tuft of cotton situated at the bottom of a 5.0 ml screw-top glass vial, then loosely twisting the cap in place. Communal eggs were housed together on cotton inside a similar vial. Both groups were kept under the environmental regimen mentioned earlier until the animals in the communal group moved upward; ascension signalled the onset of communal web construction.

For each treatment group, these observations were recorded and tabulated: eggs hatched, eggs not hatched; live first instars, dead first instars; live second instars, dead second instars. Five egg masses were individually analyzed in this fashion. The association between the rearing conditions and the viability of a developmental stage was tested by using a two-way contingency table (Sokal and Rohlf 1973).

Isolation Experiments.—The first of two experiments, in February, used an egg sac containing 700 eggs; the second, in March, used a sac with 507 eggs. Each egg sac was dissected; some of its eggs were reared singly, the remaining ones together, as the previous section described.

In experiment one, three treatment groups were set up by selecting animals raised in either the communal or the isolated manner. At the onset of communal web formation,

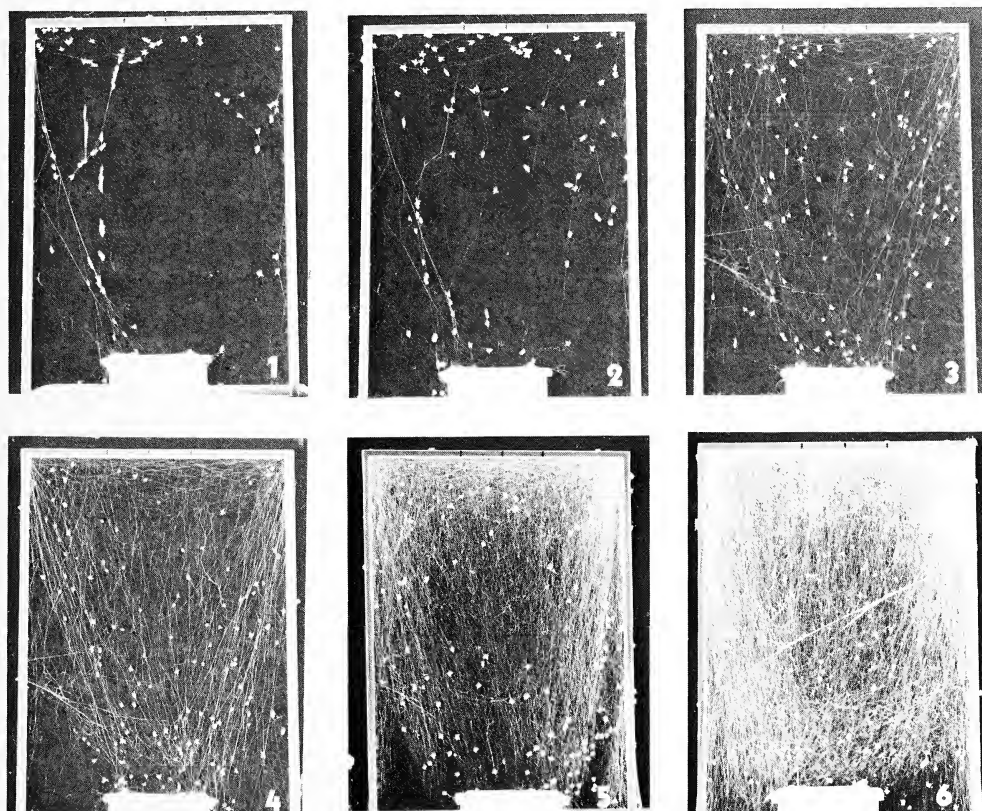


Fig. 1-6.—Time series showing construction of communal web by *Araneus diadematus* spiderlings: 1, 30 sec; 2, 60 sec; 3, 5 min; 4, 25 min; 5, 5 hr; 6, 24 hr. Spiderlings show up as white dots, silk as white lines. Calculations have shown that the spatial pattern changes over time. The rectangular frames are 13 cm wide and 18 cm high.

30 spiderlings were taken in haphazard fashion from the animals reared communally; each was moved to a wooden frame (18x13 cm, hwx) and individually contained in a translucent, polyethylene pail sealed by a snap-on cover. These animals composed the precommunal group—a name stressing their lack of experience in both constructing and inhabiting the communal web. The remainder of the spiderlings raised in the communal fashion were collectively released onto a single frame to build the communal web, and were kept together in a polyethylene pail for four days; 50 of these animals (the communal group) were randomly selected and housed singly. The third group was comprised of 50 isolated spiderlings (the isolated group). These animals were taken from their vials and likewise individually housed.

Isolated and communal treatment groups were also established in experiment two. A third group was set up too: the confined isolate group. These were animals reared in isolation and confined in their vials during the interim of four days when communal animals coexisted on common threads. Fifty such spiderlings were chosen and individually housed as before.

The webs of each group member were photographed daily (Fig. 7). Web measures were calculated from photographs of the second web constructed by each spiderling. The calibration of these photographs and the derivation of the 25 web measures have been previously described (Witt *et al.* 1968).

Web measures evaluated the size, fine structure, regularity, and shape of the web. Size measures (number of radii; median angle; number of spirals, West, North, East, and South; spiral area; center area; frame area; thread length) reflected the spatial extent and number of thread elements. Three fine structure measure (mesh width; median mesh size, North and South) expressed the density of threads in the spiral area. Nine regularity measures (oversized angles; standard deviation of central angles; angle regularity; relative deviation of spiral turns, West, North, East, and South; standard error of median mesh size, North and South) assessed the variability of thread placements. Variations in the elliptical form of the web and in the symmetry of hub location were detected by three shape measures (width over length; radius North over South; radius East over West). All these measures are defined in Witt *et al.* (1968).

Non-geometrical data were also collected in experiments one and two. The micrograms of protein in a spiderling's second web was determined using the method of Lowry *et al.* (1951). The time elapsed in days between the placement of an animal in its polyethylene pail and the fabrication of its first web was recorded.

After containment in a polyethylene pail, a spiderling was fed a gnat (*Hippelates pusio*) in its first web, and afterward in alternate webs. Water was sprayed as a fine mist into the pail every other day.

For each isolation experiment, the 27 measurements (web measures and non-geometrical data) made on all second webs were used to construct a lower triangular correlation matrix (Burch 1977). These two matrices were individually analyzed by factor analysis: each correlation matrix was factored by a principal component analysis (Harman 1967); next the resultant principal component matrix was orthogonally rotated according to Kaiser's varimax criterion (Kaiser 1958). The rotation produced a factor matrix: a set of columnar factors. The number of factors retained in the matrix was decided by the eigenvalue-one rule (Rummel 1970). Pooling the data from both experiments for a single factor analysis was avoided because: a) the treatment regime between experiments was different; b) a period of one month passed from the start of the first experiment to the

start of the second. Calculations of the factor analyses were carried out on computer programs developed by John Sall (Barr *et al.* 1975).

Factor analysis served two purposes. First, it clarified the complex interrelationships among the 27 web measurements—in the factor matrix, each factor was correlated with and so could be interpreted as a distinctive pattern of the original measurements. A measurement whose factor loading (correlation coefficient between measurement and factor) exceeded an absolute value of 0.32 was judged important for interpretative purposes; in such a case, the factor accounts for more than 10% of the measurement's variance. Second, it simplified the data by reducing a large number of correlated web measurements to a smaller number of uncorrelated variables (the factor scores). A spiderling's second web could then be described by factor scores instead of the correlated measurements. These scores were calculated by the method of regression (Rummel 1970).

If two factors from different experiments showed similar patterns of correlation with the original measurements, they were compared through the coefficient of congruence

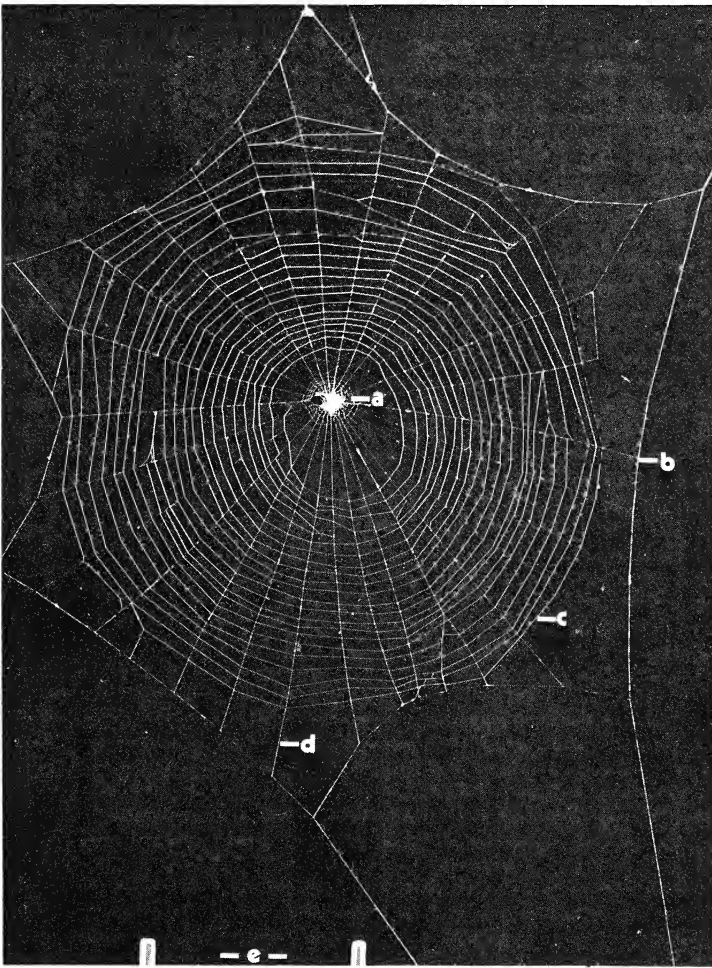


Fig. 7.—Typical orb web identifying principal constituents: hub(a), frame(b), spiral(c), radius(d), standard measuring 20 mm between prongs(e).

(Harman 1967). It measures not only pattern similarity but also magnitude similarity, and behaves like a correlation coefficient ranging from -1.00 (for perfect negative similarity) through zero (for complete dissimilarity), to 1.00 (for perfect similarity).

For each factor, a univariate analysis of variance (Sokal and Rohlf 1973) was performed on the factor scores to test the null hypothesis that the means of the treatment groups were equal. If the null hypothesis was rejected, the Least Significant Difference (LSD) method of multiple comparison (Snedecor and Cochran 1967) detected which pair(s) of means differed significantly.

Spatial Pattern Experiments.—Ten egg sacs were used in the spatial analysis. Each was prepared for observation by the method described for rearing communal spiderlings. When communal web formation seemed imminent for a given egg mass, the emergine spiderlings were permitted to fabricate this structure on the standard rectangular frame. Web and inhabitants were confined at that time in a polyethylene pail and afterwards were carefully removed at 24 hr intervals for web photography (Witt *et al.* 1968). Photographs were taken over a four day period. The number of spiderlings on a given web ranged from 10 to 500.

Nearest-neighbor distance for each spiderling was evaluated from 35 mm negatives. A negative was inserted into a slide projector, shown against a grid background whose square of unit size measured 1 mm along an edge, and enlarged to twice life size. An animal's location was recorded in Cartesian coordinates; these coordinates were analyzed by a computer program whose output included the nearest-neighbor distance for each animal.

Establishing the position of a spiderling in such a two dimensional coordinate system presupposes that the communal web exists in a single plane. Compelling the emerging animals to moor their threads to the planar wooden frame insures that the resulting web conformation approximates this desired planarity.

The distance between an individual and its nearest neighbor provides the basis for a measure of spatial pattern. A set of such distances was measured from the daily photograph of a given spiderling group; from this the mean nearest neighbor distance was calculated. The mean nearest neighbor distance expected if the members of this group were randomly distributed was also computed; Clark and Evans (1954) have shown this value to be $1/2\sqrt{\rho}$ where ρ is the density of the observed distribution expressed as the number of individuals per unit of area. The ratio of the observed mean distance to this expected mean distance, known as the R ratio (Clark and Evans 1954), evaluated spatial pattern: it assumes values less than 1 for aggregated populations, the value 1 for a random arrangement, and values greater than 1 in uniform populations.

A two-factor analysis of variance was calculated using the R values. The factors investigated were time (days 1-4) and spiderling group size (large, 50 animals or more; small, less than 50 spiderlings). In this analysis of variance model, time was considered a within-subjects variable, and spiderling group size a between-subjects variable (Myers 1972).

Humidity Experiments.—Inside a number of rectangular glass chambers (102x102x203 mm, lxwxh), a series of discrete relative humidities was maintained through saturated salt solutions; the salt solutions used and the relative humidities produced at 22°C (Winston and Bates 1960) were: LiCl · H₂O, 12.3%; MgCl₂ · 6H₂O, 32.8%; Na₂Cr₂O₇ · H₂O, 53.9%; NaCl, 75.8%; Pb(NO₃)₂, 96.4%. These particular salt solutions afford the advantage that their associated humidities are invariant over a considerable temperature range. Humidities were verified using the salt deliquescence method (Winston and Bates 1960).

Square screen platforms (90x90 mm) resting on four pieces of polyethylene tubing, one heat-fused at each corner, supported balsa wood frames (115x75 mm, hwx) above the level of salt solution in each container. Having lived on their communal web for one day, individual spiderlings from a single egg sac were haphazardly chosen and randomly assigned to one of the five humidity chambers until each contained 30 animals. The top of every chamber was then sealed airtight; after 18 hr the animals on their webs were photographed through the glass. Kodak Plus-X film was used. The entire experiment was repeated with the offspring from another egg sac.

Nearest-neighbor analysis and the R index were employed to describe the spatial pattern at each relative humidity. The trend of R values over humidity was tested for significance (Cooper 1975).

RESULTS

Rearing Experiments.—For most cocoons, the isolated eggs hatched in higher percentage than their communal counterparts did. However, the percentage of surviving first and second instars was generally lower among isolated animals than among the corresponding communal group. These results are shown in Table 1.

Statistical tests showed a significant association between the rearing conditions and the viability of specific developmental stages. Using additive data over all egg masses, a two-way contingency table classified eggs according to whether they hatched or not, and also by treatment. These data indicate that isolated eggs were more successful at hatching than their communal counterparts ($\chi^2=27.7$, $P<0.001$, $df=1$). A similar table tabulated the survival of the first and second instars with their treatments; isolated spiderlings died more frequently than communal animals did ($\chi^2=16.6$, $P<0.001$, $df=1$).

Isolation Experiments.—The resultant factors and their loadings are shown for isolation experiments 1 and 2 respectively in Tables 2 and 3. In experiment 1, seven

Table 1.—Differences between isolated and communal treatments in the viabilities of eggs and spiderlings. In most cocoons, the percentage of isolated eggs that hatched was greater than the percentage of communal eggs that hatched. Conversely, communal spiderlings generally survived in higher percentage than isolated spiderlings survived. Cocoons are specified by uppercase letters. The values in parentheses are the percentages of nonviable organisms to the total observed for the given treatment and developmental stage. The data headed "spiderlings" are additive for first and second instars.

Cocoon	Treatment	Eggs		Spiderlings	
		Hatched	Not Hatched	Live	Dead
A	Communal	382	5(1.3)	382	0(0.0)
	Isolated	115	5(4.2)	109	6(5.2)
B	Communal	33	804(96.1)	28	5(15.2)
	Isolated	7	93(93.0)	7	0(0.0)
C	Communal	164	504(75.4)	163	1(0.6)
	Isolated	24	115(82.7)	24	0(0.0)
D	Communal	200	367(64.7)	198	2(1.0)
	Isolated	57	63(52.5)	55	2(3.5)
E	Communal	68	662(90.7)	49	19(27.9)
	Isolated	16	94(85.4)	3	13(81.2)

Table 2.—From the data of isolation experiment 1, seven factors were calculated through principal components then rotated by the varimax criterion. Factors are named in the text. Variance extracted is the percent of total variance in the data removed by a specific factor. Communality is the proportion of a measurement's variance accounted for by all factors. Abbreviated: No-Rad=number of radii; Med-Ang=median angle; Spiral-W, -N, -S, -E=number of spirals West, North, South, East; Spiral=spiral area; Center=center area; Frame=frame area; Thread=thread length; Os-Ang=oversized angles; SD-C=Ang=standard deviation of central angles; Ang-Reg=angle regularity; Dev-Sp-W, -N, -E, -S=relative deviation of spiral turns West, North, East, South; Msh-SE-N, -S=standard error of median mesh size North, South; Mesh-Wdh=mesh width; Mesh-N, -S=median mesh size North, South; Wdh-Lgth=width over length; Rad-N-S=radius North over South; Rad-E-W=radius East over West; Protein=micrograms of protein in second web; Time-2=time elapsed before construction of second web. Loadings greater than or equal to an absolute value of 0.32 are shown in parentheses.

Factors:	1	2	3	4	5	6	7	
Variance extracted:	25.9	10.4	9.9	6.6	7.3	11.8	5.0	Total=76.9%
Web measurements	Factor loadings							Communality
No-Rad	(.80)	.13	(-.38)	.11	-.12	-.21	-.05	.88
Med-Ang	(-.76)	-.19	.31	-.20	.20	.26	.08	.87
Spiral-W	(.81)	-.05	-.07	(.46)	-.01	-.01	-.05	.88
Spiral-N	(.88)	-.12	-.07	.10	.11	-.13	.20	.87
Spiral-S	(.92)	-.10	-.10	-.08	-.02	-.04	-.21	.92
Spiral-E	(.88)	-.17	.01	.13	.13	-.02	.02	.85
Spiral	(.84)	(.34)	-.10	.04	-.12	(.32)	-.10	.95
Center	(.44)	.15	-.25	-.00	(-.47)	(.41)	-.15	.69
Frame	-.06	.31	.14	.12	(-.67)	.12	-.03	.60
Thread	(.96)	.09	-.13	.10	-.09	.13	-.08	.99
Os-Ang	.11	.15	(.80)	-.03	-.18	-.18	.20	.78
SD-C-Ang	(.42)	-.05	(.84)	-.12	.01	.05	-.07	.91
Ang-Reg	(-.39)	-.09	(.87)	-.07	.02	.03	-.01	.92
Dev-Sp-W	.25	(.67)	-.02	-.07	-.06	.14	.06	.54
Dev-Sp-N	-.03	.30	.27	-.28	(-.60)	.22	.17	.69
Dev-Sp-E	-.06	(.69)	.02	.06	-.14	.14	-.11	.53
Dev-Sp-S	-.05	(.76)	-.03	.04	-.09	.19	-.10	.63
Msh-SE-N	-.31	(.32)	.16	-.25	(-.43)	(.54)	.10	.77
Msh-SE-S	(-.43)	(.45)	.04	.17	.13	(.39)	.12	.59
Mesh-Wdh	.03	(.58)	.05	-.00	-.18	(.73)	-.13	.93
Mesh-N	-.07	.12	-.03	-.07	-.14	(.84)	.03	.76
Mesh-S	.03	.25	-.08	-.09	.08	(.85)	-.03	.80
Wdh-Lgth	.14	.09	-.02	(.81)	.16	-.17	-.04	.74
Rad-N-S	-.08	-.21	.10	.05	-.21	.09	(.86)	.85
Rad-E-W	.19	.00	-.12	(.70)	-.14	-.00	-.01	.56
Protein	.17	-.10	-.01	.31	(-.35)	.29	(-.56)	.65
Time-2	-.30	.27	.24	-.04	(.55)	.29	-.13	.62

uncorrelated factors accounted for 76.9% of the variance in the 27 web measurements. Eight factors explained 80.8% of the data's variance in experiment 2.

The tables also list, for each web measurement, the proportion of its variance that is explained by the factors removed. The explained variance of a measurement is called its communality. Among all variables, the variation in thread length was the one most completely described by each factor set; least explained were relative deviations of spiral turns East in experiment 1 and frame area in experiment 2.

A particular factor generated from the data of one experiment often resembled in its pattern and magnitudes of loading a factor or factors generated from the data of the

other. Therefore the naming and interpreting of similar factors can economically be discussed together rather than piecemeal.

In both factor analyses, each of the first factors loaded positively on the measures of web size. The coefficient of congruence (symbolized by the Greek letter delta) between the two was high ($\delta=+0.95$). So they were given the same name: 'web size' factor. Presumably such a factor represents the number of filamentous components in the web.

As shown in the factor matrix of the first experiment, factor 2 was associated with measurements of web regularity and factor 6 with measurements of fine structure. The three largest coefficients of factor 2 were linked to the regularity of spiral placement—relative deviation of spiral turns South, East, and West (loading on this measure in the North almost reached criterion). Factor 2 was called 'spiral irregularity'. The major loadings of factor 6 were on the three measurements of fine structure (mesh width; median mesh size, North and South). In addition, this factor showed substantial association with the standard error of median mesh size, North and South. Accordingly, it reflected 'mesh size and irregularity'.

Factor 2 in the matrix of the second experiment appeared to be a composite of both regularity and fine structure measurements. As expected, it resembled the 'mesh size and irregularity' and the 'spiral irregularity' factors, its respective coefficient of congruence with each being $+0.74$ and $+0.72$. This factor was named 'mesh size and spiral irregularity'.

Factor 3 of experiment 1 loaded distinctly on the three measurements concerned with the regularity of radial thread arrangement (oversized angles, angle regularity, and standard deviation of central angles). It revealed a striking likeness to factor 4 of experiment 2 ($\delta=+0.82$). Both factors were named 'central angle irregularity'.

Measurements of web shape dominated the loadings in factor 4 of experiment 1. The coefficients of this factor in diminishing rank were width over length, radius East over West, and number of spiral turns West. These are all measurements of web symmetry, viz., as it regards hub location. Factor 4 was called 'hub symmetry'. Except for sign reversals, it was similar to factor 8 of experiment 2 ($\delta=-0.72$), and so the latter entitled 'hub asymmetry'.

Showing little similarity to any factor of the second experiment, factor 5 from experiment 1 displayed a confusing mixture of coefficients. It was characterized by large negative loadings on two size measurements, frame and center areas, by negative loading on two regularity measurements, relative deviation of spiral turns North and standard error of median mesh size North, by a positive association with time before web construction, and by a negative loading on the protein content of the web. This factor was labeled 'time-associated size and irregularity diminution' and probably reflected web changes caused by malnutrition in spiderlings who delayed the onset of orb weaving.

Factors denoting the vertical and lateral location of the web's hub were discovered in both factor analyses. Factor 7 of experiment 1 loaded in bipolar fashion: positively with radius North over South, and negatively with protein content of the web. It was named 'vertical hub symmetry vs. protein'. Factor 3 of experiment 2 resembled factor 7 ($\delta=+0.66$); it differed from factor 7 by failing to show a large inverse relationship with protein contained in the web, and was therefore dubbed 'vertical hub symmetry'. Another factor from experiment 2, factor 6, showed some likeness to the 'vertical hub symmetry vs. protein' factor ($\delta=+0.36$). Having loaded positively on both radius East over West and frame area, and negatively on the protein content of the web, it was named 'lateral hub symmetry vs. protein'.

Table 3.—The factor matrix for the data of isolation experiment 2 comprised eight factors. Details are explained in Table 2.

Factors:	1	2	3	4	5	6	7	8	
Variance extracted:	28.2	15.0	5.1	6.4	7.1	4.4	9.1	5.5	Total=80.8%
Web measurements	Factor loadings								Communality
No-Rad	(.91)	-.23	-.01	-.02	-.02	-.01	-.01	-.08	.89
Med-Ang	(-.89)	.17	.01	-.02	.91	-.04	.01	.13	.83
Spiral-W	(.84)	-.26	.09	-.07	.11	.06	.12	-.13	.84
Spiral-N	(.80)	(-.33)	.12	-.10	.20	-.03	.25	.07	.88
Spiral-S	(.81)	-.10	-.23	-.03	-.10	-.07	(.43)	.13	.93
Spiral-E	(.81)	-.23	-.05	-.12	.04	-.04	(.40)	-.04	.88
Spiral	(.87)	.30	-.09	.03	.23	-.07	.01	-.08	.93
Center	(.34)	.03	.02	.06	(.76)	-.17	-.08	-.02	.74
Frame	-.05	(.63)	-.08	-.01	.23	(.34)	.06	-.02	.57
Thread	(.95)	-.00	-.07	-.01	.19	-.06	.18	-.02	.97
Os-Ang	.02	-.01	-.00	(.92)	-.08	.03	-.01	-.10	.86
SD-C-Ang	(-.67)	.27	-.04	(.58)	-.04	.07	.03	.02	.87
Ang-Reg	(-.64)	.25	.06	(.60)	.01	.05	.06	.04	.86
Dev-Sp-W	.04	(.57)	(-.34)	.01	-.14	.13	-.20	(-.49)	.76
Dev-Sp-N	-.14	(.79)	.28	-.12	-.14	.04	-.16	.28	.86
Dev-Sp-E	-.15	(.56)	-.09	.16	.02	-.22	(-.49)	-.03	.66
Dev-Sp-S	-.15	.22	-.27	-.06	-.01	.12	(-.78)	.06	.78
Msh-SE-N	(-.42)	(.75)	.18	.07	-.10	.01	-.18	.15	.83
Msh-SE-S	-.28	.18	.08	-.03	.17	.16	(-.83)	.08	.84
Mesh-Wdh	-.14	(.83)	-.16	.10	.27	-.13	-.30	-.14	.94
Mesh-N	-.26	(.65)	.01	.19	.24	-.24	-.05	-.03	.64
Mesh-S	-.04	(.32)	-.09	-.15	(.75)	-.09	-.26	-.10	.78
Wdh-Lgth	.13	-.09	.02	.08	.04	-.02	.13	(-.90)	.87
Rad-N-S	-.10	.03	(.93)	.01	-.00	-.03	.12	.01	.89
Rad-E-W	(.35)	.00	.18	.01	-.12	(.58)	-.24	(-.37)	.70
Protein	(.34)	.04	.13	-.09	.08	(-.67)	.02	-.10	.61
Time-2	-.23	.06	-.13	.12	(-.57)	-.27	(-.33)	-.23	.64

Two factors of experiment 2 described time-dependent changes in web structure; various details of size became smaller and of fine structure irregular when the spiderling postponed the fabrication of its web. Factor 5 was characterized by positive coefficients associated with center area and median mesh size South (mesh-S), and a negative loading on time elapsed before web construction. It was subsequently termed 'time vs. center and mesh-S'. The three largest loadings of factor 7, all negative, were: standard error of median mesh size South, and relative deviation of spiral turns South and East. This factor also correlated positively with the number of spiral turns South and East, and inversely with time elapsed before web construction. It was recognized as 'time vs. spiral regularity, South and East'.

For each factor, a statistical summary (N , \bar{x} , $SD_{\bar{x}}$) of its scores, by treatment, together with the results of a univariate analysis of variance, across treatments, is presented in Table 4. Significant F-ratios ($P < 0.05$) were detected in two factors of experiment 1: 'spiral irregularity' and 'vertical hub symmetry vs. protein'. In experiment 2, 'mesh size and spiral irregularity' when tested gave a significant F-value.

A posteriori comparisons of the treatment groups for the three preceding factors uncovered these differences. Regarding 'spiral irregularity', the isolated animals built webs

that were more regular in the placement of spiral threads than were the webs built by their communal counterparts. Scores on the 'vertical hub symmetry vs. protein' factor showed two things. First, isolates constructed webs containing less protein than webs constructed by communal or precommunal animals. Second, they situated the hubs of these webs more centrally along the vertical axis than the hubs situated by spiderlings of the other groups. Finally, analysis of the results from the 'mesh size and spiral irregularity' factor revealed that the confined isolates wove webs with greater regularity in spiral placement and with smaller mesh size than seen in the webs of their isolate or communal counterparts.

Spatial Pattern Experiments.—The spatial patterns taken by large groups of spiderlings did not differ from the patterns taken by small groups ($F=1.94$, $df=1$, N.S.). And group size and time did not interact significantly ($F=1.59$, $df=3$, N.S.). The arrangement in space of a group of spiderlings changed, however, over time ($F=5.64$, $df=3$, $P<0.005$). For each day, the R values from the two sizes of groups were pooled, and the mean was calculated. Mean R values for days 1-4 were respectively: 0.756, 0.860, 0.934, 0.957. Over this series of values, Cooper's test (1975) for increasing trend was significant ($P<0.02$): the spiderlings drew apart from one another over time, moving from an aggregative towards a random arrangement.

Humidity Experiments.—For humidities 12.3% through 96.4%, the respective R values are shown below; each series corresponds to an experimental replication: 0.780, 0.747, 0.640, 0.706, 0.539; 0.599, 0.452, 0.512, 0.374, 0.300. Animals aggregated at all humidities. Trend tests (Cooper 1975) performed on each data set were significant ($P<0.015$). R values decreased as humidity increased, i.e., the spiderlings drew together when the humidity went higher.

DISCUSSION

Several hypotheses can explain why isolated eggs showed a lower mortality than communal eggs showed. An inviting hypothesis posits the influence of a contagious factor, e.g., a pathogenic microorganism (Cloudsley-Thompson 1968) that spreads through the communal context. Another explanation is supported by two pieces of circumstantial evidence: 1) the second instar spiderlings within the egg sac were sometimes seen to clutch unhatched ova; 2) second instars emerging from the egg sac were often visibly different in their sizes. These observations imply that second instars could have fed on unhatched ova; Valerio (1974) describes the occurrence of this phenomenon among second instars of the American House Spider (*Achaearanea tepidariorum* Koch). Or possibly the high mortality of communal eggs resulted simply from overcrowding. However, females of *Araneus diadematus* Clerck normally lay their egg sacs in cramped surrounding, e.g., out-of-the-way crevices beneath peeling bark (McCook 1890), where conditions of space, ventilation, and humidity could be more harmful than those in the laboratory.

Probably nowhere is isolation more drastic in consequence than among the social insects; hive-bees, ants, and termites, when isolated, survive only a few hours, or at most a few days (Chauvin 1967). My study showed that the spiderlings could be reared in isolation in the laboratory, but it also pointed out a statistical association between viability and rearing condition.

Why did isolated spiderlings die more frequently than communal spiderlings did? Since this question was not examined directly by experiment, its answer can only be speculated

Table 4.—Descriptive statistics, Least Significant Difference tests (LSD), and Analysis of Variance (ANOVA) for the factor scores of the first (1) and second (2) isolation experiments. Factors are listed in the order of discussion under RESULTS. Scores for a given factor were collectively standardized to a mean of 0.5 and a variance of 1.0. No significant difference ($P < 0.05$, LSD test) exists between means labeled with the same symbol (*, #). Abbreviated: \bar{x} =mean; $SD_{\bar{x}}$ =standard error. The number of spiderlings (N) in the treatment groups were confined isolate, N=43; isolate, N=37; communal, N=40; precommunal, N=28.

Factors	Experiment	Treatment Groups				ANOVA	
		Confined Isolate	Isolate	Communal	Precommunal	F value	Prob>F
Web size	1	\bar{x}	0.46	0.37	0.74	1.14	0.32
	2	$SD_{\bar{x}}$	0.179	0.154	0.167		
Spiral irregularity	1	\bar{x}	0.77	0.49	—	1.79	0.17
	2	$SD_{\bar{x}}$	0.158	0.164	—		
Mesh size and irregularity	1	il 3,—	0.172	0.82 #	0.38* #	3.68	0.03
	2	\bar{x}	0.168	0.148	0.180		
Mesh size and spiral irregularity	1	\bar{x}	0.23	0.54	0.80	2.80	0.06
	2	$SD_{\bar{x}}$	0.123	0.164	0.217		
Central angle irregularity	1	0.19 #	0.74 *	0.67 *	—	3.66	0.03
	2	0.155	0.188	0.145	—		
Hub symmetry	1	\bar{x}	0.62	0.41	0.47	0.41	0.67
	2	$SD_{\bar{x}}$	0.156	0.145	0.221		
Hub asymmetry	1	0.48	0.42	0.58	—	0.22	0.81
	2	0.159	0.171	0.170	—		
Time-associated size and irregularity diminution	1	\bar{x}	0.30	0.54	0.70	1.32	0.27
	2	$SD_{\bar{x}}$	0.174	0.160	0.164		
Vertical hub symmetry vs. protein	1	0.61	0.42	0.43	—	0.46	0.64
	2	0.185	0.160	0.132	—		
Vertical hub symmetry	1	\bar{x}	0.41	0.70	0.33	1.37	0.26
	2	$SD_{\bar{x}}$	0.148	0.158	0.205		
Lateral hub symmetry vs. protein	1	0.83 *	0.83 *	0.38 #	0.24 #	3.37	0.04
	2	0.133	0.161	0.208	—		
Time vs. center and median mesh size South	1	0.50	0.44	0.55	—	0.10	0.90
	2	0.160	0.170	0.171	—		
Time vs. spiral regularity South and East	1	0.69	0.40	0.35	—	1.30	0.28
	2	0.157	0.175	0.164	—		
	1	0.51	0.20	0.75	—	2.60	0.08
	2	0.162	0.153	0.168	—		
	1	0.69	0.32	0.42	—	1.45	0.24
	2	0.156	0.187	0.155	—		

on. Others have noted the same phenomenon. Darchen (1965) reared social spiderlings (*Agelena consociata* Denis) in isolation and observed that these animals died sooner than did group-reared young; he attributed their reduced longevity to the absence of either inter-individual contacts or trophallaxis. Studying the same spider, Krafft (1971) made similar findings. His isolated animals did not live so long or grow so large as animals that were reared in groups. In my study, the most noticeable behavior of grouped animals inside the cocoon was their frequent touching of one another. Whether such tactile stimulation can account for the difference in viabilities should be tested.

The calculations of the factor analyses made possible an economical and concise description of the structure of the orb web. Generally speaking, the generated factors described a web in five ways. Classifications a) through e) progress from the most important to the least important in explaining the variance of the experimental data: a) overall size: the total number of filamentous segments in the web (or possible the sum of the quadrilaterals that make up the catching zone); b) mesh size and its variation (a mesh is the trapezoid shape formed by two adjacent radii and two adjacent spirals); c) irregularity of spiral thread placement; d) irregularity of radial thread placement (another way of saying 'central angle irregularity'); e) the lateral and vertical symmetries of the hub. Witt and Reed (1965) made a less detailed factor analysis of some of the 27 web measurements. They also identified factors related to web size, mesh width, and hub symmetry.

As the factor scores from the isolation experiments showed, the second orb webs woven by isolates were not very different in their geometry (and possible function) from similar structures built by their communal litter-mates. Because the isolates neither constructed nor occupied the communal web, such experience can be judged unnecessary for the development of normal orb-weaving behavior. This developmental homeostasis (Mayr 1974, Alcock 1975) would seem advantageous to the short-lived spider, for whom, early in life, the orb web is essential to secure prey.

The physiological basis of such development probably resides in the maturation of the central body. This structure is a flat neuropilar sheet that stretches across the posterior part of the spider's brain. Babu (1975) found a correspondence in time between the formation of the central body and the start of orb-weaving behaviors in the second instar.

Other workers have performed isolation experiments. Petrusiewiczowa (1938) and Mayer (1953) isolated spiderlings *after* their communal web association, and reared them in small tubes that prevented web-building behavior. When released, these animals constructed seemingly normal webs on their first attempt. Using a similar experimental approach, Witt *et al.* (1970) found that spiders confined in narrow glass tubes after the communal web phase, and then released for several days afterwards built webs whose size measures (thread length, spiral area, numbers of radii and spiral turns) were significantly less than those of the control group; these size measures could be brought to control levels by a preliminary pulling of thread that partially emptied the spider's silk glands. This diminution was not observed in the webs of my solitary animals, probably because my confinement period was shorter and less restrictive.

The primary geometrical difference distinguishing the webs of solitary from group-reared animals was the solitary spiders' greater regularity in spiral thread placement, through secondary differences also included their more central hub location and smaller mesh size. All of the above web measures change progressively as a spider ages (Witt *et al.* 1968, Witt *et al.* 1972, Risch 1977): spiral placement becomes more irregular, hub location more asymmetric, and mesh size increases. Interpreted in this context, one

might say that the spiderlings reared in groups matured more rapidly than the isolates matured.

These 'group effects', as they influence viability and maturation, are commonplace among the insects (Chauvin 1967, Cotter 1974). In spiders, Krafft (1971) observed that 'group effects' among the young of the communally living spider *Agelena consociata* resulted in a reduction of the intermolt period and a growth acceleration.

Because the treatment effects in the isolation experiments were minor, the factor analysis can be interpreted from yet another perspective. It suggests what elements natural selection might modify to adapt the spiderling to a changing environment. Of the five classes of factors, those associated with overall web size and with mesh size represented the two greatest sources of variation observed in the second webs of spiderlings. Those associated with irregularity in thread placement and with hub symmetry accounted for smaller sources.

Witt and Ralings (1973) have calculated heritabilities (broad sense) for some of the 27 web measurements from the cross spider. Their values of heritability paralleled the levels of phenotypic variation in the five classes of factors. All size measurements—radii number, number of spirals in the four cardinal directions, frame area, spiral area, center area, and thread length—showed high heritabilities (they were under strong genetic control). The heritabilities of measurements of mesh size were significantly different from zero but about half as large as those for measurements of web size. Finally, there was little or no evidence of genetic control for those web characteristics measuring the irregularities of thread placement and those measuring the symmetry of the hub.

Both kinds of information, phenotypic variation and heritabilities, suggest which web structures natural selection is most likely to modify. It seems to be placing a premium on varying web size and mesh size to adapt the spiderling to a changing environment. But it tolerates little variation in the irregularity of thread placement and in hub symmetry. Risch (1977) reached similar conclusions about the evolution of the web of the adult cross spider.

Finally, the factors have two potential meanings for the biology of the spider. But both need independent confirmation. The first is related to the most obvious purpose of the web for the spiderling: catching prey. Could these factors be important elements in making the web an efficient trap? Some evidence supports them in this role.

Witt *et al.* (1968) argued that web and mesh sizes are important in prey capture. A larger web covers a wider area in which flying insects can get caught. Mesh size limits the size of prey that the web can trap: insects that are too large or too small escape. For the catching zone to be effective at all points, reason suggests that the placement of spirals must be regular. Regular arrangement is also necessary for radial threads because they provide the only avenues for the spider to approach and retrieve prey from the catching zone. Finally, the location of the hub within the web can determine how fast the spider gets to its potential prey. For example, will the spider's approach be assisted or hindered by gravity, and over what fraction of the spiral area will its approach be assisted or hindered?

A second potential meaning of factor analysis for the biology of the spider is understanding the internal organization of web-building behavior. A given factor has high loadings for a number of behavioral measurements. If independent evidence also suggests that these same measurements are related to one another and possibly to common internal causes, then the factor could represent an internal organization of behavior (e.g., a neural structure) common to each of these measured behaviors (Huntingford 1976).

Factors that describe web size and those that describe regularity of thread placement hint at the existence of respective internal centers for these behaviors. Support is two-fold. Comparative histological studies have revealed that the central body of the brain is a neural center important in the operation of web-building behavior (Bullock and Horridge 1965). Witt *et al.* (1964) made random lesions in the brains of cross spiders. Some of these animals built webs smaller in size than webs built before treatment; others wove webs similar in size to control webs but altered in regularity.

Nearest-neighbor measurements made during the spatial pattern experiment provided mathematical support for the spiderlings' aggregation on the communal web. Whether the spiderlings group together because of an interattraction between individuals or through the influence of extrinsic conditions, remains a fine distinction not resolved by these experiments. Since homogeneous surroundings were provided for the spiderlings, and because the R index evaluates spatial pattern at a small scale (Pielou 1969), one not likely to be affected by large-scale environment factors, the interattraction explanation is certainly credible.

Grouping on the communal threads, as measured by the R index, becomes less pronounced with time. The increase of inter-sib aggressiveness over time (Bristowe 1939), Mayer 1953, Meier 1967) or the gradual exhaustion of a spiderling's yolk reserve or both could enhance dispersal via triggering aggressive behavior; e.g., hermit crabs show heightened levels of aggression when starved (Hazlett 1966).

Meteorological factors, especially wind velocity and temperature (van Wingerden and Vugts 1974), could promote or inhibit dispersal. Variability in these factors might account for the temporal discrepancies noted by all observers between emergence from the egg sac and ballooning behavior.

On the communal web, as shown by the humidity experiments, *Araneus diadematus* spiderlings tend to spread apart at low humidities and come together at high humidities. Though such behavior appears paradoxical as regards water balance, it may represent a proper survival strategy during rainstorms. In such weather, single animals who wander or balloon away from the web could easily drown. Observations by Robinson and Robinson (1973) support this hypothesis. They noted that communal spiderlings of the orb-weaver *Nephila maculata* Fabricius, during the rainy season of New Guinea, associate into a compact ball of animals near the center of their communal structure.

How does the communal web fit as a stage in the ontogenetic development of web-building behavior? Oppenheim (1978) concludes that there are two equally important (and usually mutually exclusive) goals of ontogenetic development: the first is the gradual step-by-step building of an adult organism that can breed successfully to ensure the survival of the species (principle of developmental continuity); the second is to assure that an organism is, at each point in its development, adapted to the peculiarities of its environment (developmental discontinuity). In the second case, he emphasizes that structures or behaviors that are adaptive at one stage might be inappropriate to normal functioning in a different environment at a later stage. So, they would be suppressed, modified, or discarded altogether. Because the communal web is evidently not a training ground where spiderlings practice and gradually perfect their orb-weaving behavior, it could exemplify an adaptive discontinuity in behavioral development. In what sense might it be adaptive?

Aside from its obvious function as a substratum that economically uses available space to support a large number of animals, and its potential to increase the survivorship of grouped over isolated animals, the chief role of the communal web is probably protective

in nature. This hypothesis could be tested only negatively in the laboratory. That is, since predators were excluded under laboratory conditions, the communal web stage of development appeared less important for normal maturation. Protection against predators is the adaptive advantage of group life found in the widest diversity of animals (Wilson 1975).

In nature, the communal web is a three dimensional, radiating network, and the spiderlings typically mass into a ball-shaped configuration situated centrally within this network. Such a concentration of sensory apparatuses (Galton 1883), surrounded by filaments possessing a potential to communicate the arrival of intruders, should make the detection of predators easier. Also, collective assumption of the spheroidal configuration can effectively reduce the extent of vulnerability to enemies or adverse weather (Hamilton 1971).

The communal web period can be thought of as an interim of variable duration, giving protection to the spiderling, until optimal atmospheric conditions favor its dispersion and the construction of its first orb web.

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SPERMATOPHORES OF SOME NORTH AMERICAN SCORPIONS (ARACHNIDA, SCORPIONES)

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ABSTRACT

Two basic types of scorpion spermatophores are differentiated: flagelliform and lamelliform. The pre-insemination and post-insemination flagelliform spermatophore of *Centruroides sculpturatus* Ewing (Buthidae); and lamelliform spermatophores of *Didymocentrus comondae* (Stahnke) (Diplocentridae), *Vaejovis confusus* Stahnke and *Hadrurus arizonensis* Ewing (Vaejovidae); and the post-insemination lamelliform spermatophore of *Supersitionia donensis* Stahnke (Chactidae) are described and illustrated.

Comparisons with other arachnid spermatophores reveal no similarities with the flagelliform type, while the lamelliform type of scorpions is apparently homologous to the spermatophores of atemnid pseudoscorpions.

The family Buthidae is characterized by flagelliform spermatophores, by males having a complex type of reproductive system, and females having an "eight-celled" reticular ovariterus. The families Bothriuridae, Chactidae, Diplocentridae, Scorpionidae and Vaejovidae are characterized by lamelliform spermatophores, by males having a simple type of reproductive system, and females having a "six-celled" reticular ovariterus. The spermatophore of the family Chaerilidae is unknown, males have an intermediate type of reproductive system and females have a "six-celled" type of reticular ovariterus. It is postulated that the Chaerilidae are more closely related to scorpions with lamelliform spermatophores than they are to buthids, and their spermatophores are probably of a lamelliform "type".

INTRODUCTION

Sperm transfer in scorpions is indirect, using a partially sclerotized spermatophore. This fact was originally reported, almost simultaneously, by four authors in 1955-1956. Since then, spermatophores representing 16 genera and five recent families have been described (Table 1).

The spermatophores are formed in the paraxial organs of the male reproductive system, the right paraxial organ producing the right half of the spermatophore (= hemispermaphore), and the left paraxial organ the left hemispermaphore. The hemispermaphores are mirror images of each other, and are always produced one pair at a time. During mating activities a sexually mature male locates a receptive female, grasps her pedipalps (and occasionally her chelicera), and proceeds to drag her along in his search for a suitable substrate onto which the spermatophore will be glued. This search may last for

several hours, and the behavior that the soon-to-mate pair goes through in this process has been described as a form of courtship (for a recent review see Garnier and Stockmann 1972). When the male finds a suitable substrate the hemispermatothores slide out of their respective paraxial organs, move past the genital atrium (where the hemispermatothores are glued together), and the spermatophore is attached to the substrate. The spermatophore contains the sperm mass in a concealed vesicle so that sperm are not exposed to a desiccating atmosphere. The male then pulls the female over the spermatophore, guiding her so that her genital opening reaches a position directly above the spermatophore. A brief struggle ensues and the female's rocking motion helps to engage the spermatophore with her genital operculi. Continued rocking by the female triggers spermatophore opening, and the sperm mass is transferred into her genital opening. The opening of the spermatophore often affects its overall appearance; consequently, spermatophores can be described in both the pre-insemination and post-insemination conditions.

The objectives of this contribution are to describe the pre-insemination and post-insemination spermatophores of *Centruroides sculpturatus* Ewing (Buthidae), *Didymocentrus comondae* Stahnke (Diplocentridae), *Vaejovis confusus* Stahnke and *Hadrurus arizonensis* Ewing (Vaejovidae); and the post-insemination spermatophore of *Superstitionia donensis* Stahnke (Chactidae).

MATERIALS AND METHODS

Scorpion spermatophores are not easy to obtain, especially if both the pre-insemination and post-insemination conditions are needed. A mating pair (with interlocked pedipalps) has to find a suitable substrate before the male will deposit the spermatophore. Very few people have observed scorpions mating in nature, and all published accounts of mating behavior are based on laboratory observations. Adult specimens have to be collected at the proper time and brought into the laboratory before the matings can be staged, and the spermatophores recovered. Consequently, most published spermatophore descriptions accompany and support information concerned primarily with studies on the mating behavior of scorpions, the descriptions are often quite brief, and the terminology used by different authors is variable. In addition, the difficulty of obtaining spermatophores accounts for the paucity of spermatophore descriptions both in species numbers and in the number of spermatophores examined per species.

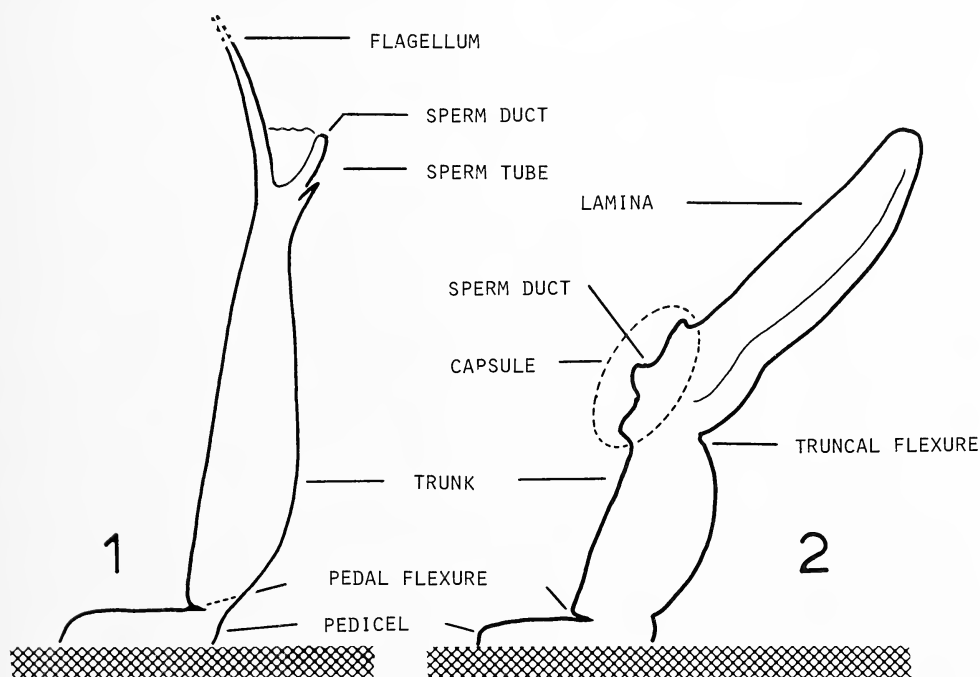
The post-insemination spermatophore of *Superstitionia donensis* described below was recovered from a laboratory-staged mating, and the description of the spermatophore of *Didymocentrus comondae* is based on five spermatophores found in the field during studies of its mating behavior. The remainder of the spermatophores described in this contribution were recovered using a different, unorthodox approach that was discovered accidentally. A small number of adult *Centruroides sculpturatus* were collected at night with the aid of an ultraviolet light, and placed temporarily in a plastic bag containing a crumpled piece of newspaper (to provide hiding places) while the search for more specimens continued. The specimens were left overnight in the bag, and the following morning, when they were separated, examination of the crumpled newspaper revealed two attached spermatophores. This procedure was then repeated, yielding 10 additional spermatophores of *C. sculpturatus*, seven of *Vaejovis confusus*, and nine of *Hadrurus arizonensis*. Although this simple technique for obtaining spermatophores has not yet

been tried on other species, it should prove successful in a number of taxa. In the absence of a suitable substrate male scorpions will attach the spermatophore to newspaper, but the females are occasionally unable to retrieve the sperm (as indicated by the presence of pre-insemination spermatophores on the newspaper available to the three species reported herein).

TERMINOLOGY

The known spermatophores belong to two types based on the appearance of the free, distal end. The two types are briefly characterized below in order to introduce the terminology used in the descriptions which follow (*italics indicate either new terminology, or the preferred term from those that have been used previously*).

Flagelliform spermatophores.—The spermatophores of buthid scorpions are flagellate, and consist of three basic parts: (a) the base, foot, or *pedicel*; (b) the basal portion, stem, or *trunk*; and (c) the *flagellum* (Fig. 1). The pedicel attaches to the substrate and is the first part to emerge from the male during deposition. The *pedal flexure* connects pedicel and trunk. The trunk is rod-like, about five to ten times longer than its diameter, and contains the sperm vesicle. Distally the trunk (a) bears the *sperm tube*, which is ornamented with hooks, tubercles, lobes, or apophyses of importance during sperm transfer, and bears the opening of the *sperm duct*; and (b) tapers into the flagellum. The flagellum is elastic, represents the free, distal end of the spermatophore, and in some species can presumably be stretched to 40 times its length (Bücherl 1956).



Figs. 1-2.—Diagrammatic comparison of scorpion spermatophores indicating the various structures and terminology used in the text: 1, flagelliform spermatophore; 2, lamelliform spermatophore.

Table 1.—List of scorpion species for which the spermatophore has been described.

	Country	References
FAMILY BUTHIDAE		
<i>Androctonus australis</i> (L.)	Algeria	Auber-Thomay 1974
<i>Buthotus judaicus</i> Simon	Israel	Shulov and Amitai 1958, 1959; Shulov 1958
<i>Buthus occitanus</i> Amoreux	France	Auber 1963
<i>Centruroides sculpturatus</i> Ewing	U.S.A.	Francke (this study)
<i>Centruroides limpidus</i> (Karsch)	Mexico	Mazzotti 1963
<i>Isometrus maculatus</i> (De Geer)	Tanzania	Probst 1972
<i>Leiurus quinquestriatus</i> (H. & E.)	Israel, Egypt	Shulov and Amitai 1958, 1959; Shulov 1958; Abushama 1968
<i>Parabuthus planicauda</i> Pocock	South Africa	Alexander 1959
<i>Rhopalurus rochai</i> Borelli	Brazil	Matthiesen 1968
<i>Tityus bahiensis</i> (Perty)	Brazil	Bücherl 1956; Matthiesen 1976
<i>Tityus trivittatus</i> Kraepelin	Brazil	Bücherl 1956
<i>Uroplectes triangulifer</i> Thorell	South Africa	Alexander 1959
FAMILY BOTHRIURIDAE		
Subfamily Bothriurinae		
<i>Bothriurus bonariensis</i> (Koch)	Uruguay	Zolessi 1956
<i>Bothriurus bucherli</i> San Martin	Uruguay	San Martin and Gambardella 1967
<i>Bothriurus flavidus</i> Kraepelin	Argentina	Abalos and Hominal 1974
<i>Urophonius iheringii</i> Pocock	Argentina	Maury 1968
Subfamily Brachistosterninae		
<i>Brachistosternus (Leptosternus)</i> sp.	Argentina	Maury 1975

FAMILY CHACTIDAE			
Subfamily Euscorpioninae			
<i>Euscorpius carpathicus</i> (L.)	Italy	Angermann 1957	
<i>Euscorpius flavicaudis</i> (De Geer)	Italy	Angermann 1957	
<i>Euscorpius italicus</i> (Herbst)	Italy	Angermann 1955, 1957; Angermann and Schaller 1956	
Subfamily Superstitioninae			
<i>Superstitionia donensis</i> Stahnke	U.S.A.	Francke (this study)	
FAMILY SCORPIONIDAE			
Subfamily Scorpioninae			
<i>Opisthophthalmus latimanus</i> (Koch)	South Africa	Alexander 1956, 1957	
FAMILY DIPLOCENTRIDAE			
Subfamily Nebinae			
<i>Nebo hierichonticus</i> (Simon)	Israel	Rosin and Shulov 1963; Shulov and Amitai 1958	
Subfamily Diplocentrinae			
<i>Didymocentrus comondae</i> (Stahnke)	Mexico	Francke (this study)	
FAMILY VAEJOVIDAE			
Subfamily Vaejovinae			
<i>Vaejovis confusus</i> Stahnke	U.S.A.	Francke (this study)	
Subfamily Hadrurinae			
<i>Hadrurus arizonensis</i> Ewing	U.S.A.	Francke (this study)	

Lamelliform spermatophores.—The spermatophores of other scorpion families studied thus far (Table 1) are lamellate “knife-like” structures having three, and occasionally four, basic parts: (a) the pedicel, (b) the trunk, (c) the *lamella*, and occasionally (d) the *capsule* (Fig. 2). The pedicel is attached to the substrate, and connects with the trunk at the pedal flexure. The trunk is usually subcircular in cross-section, about three to five times longer than its diameter, and widens gradually away from the pedicel. The trunk houses the sperm vesicle and the capsule when one is present. The capsule is a sclerotized structure ornamented with lobes, hooks, spines, or apophyses, is traversed by the sperm duct, and is everted into the genital opening of the female during insemination. Distally the trunk (a) may be ornamented with ridges, tubercles, or apophyses of importance for emptying the contents of the sperm vesicle during insemination, and (b) connects to the lamella at the *truncal flexure*. The lamella is about as long as the trunk and is blade-like, with a “blunt” and a “sharp” edge. The blunt edge faces the substrate in the pre-insemination spermatophore and is always entire, while the sharp edge faces away from the substrate and may be notched basally. The sides of the lamella can be smooth, or have longitudinal ridges somewhere along the length.

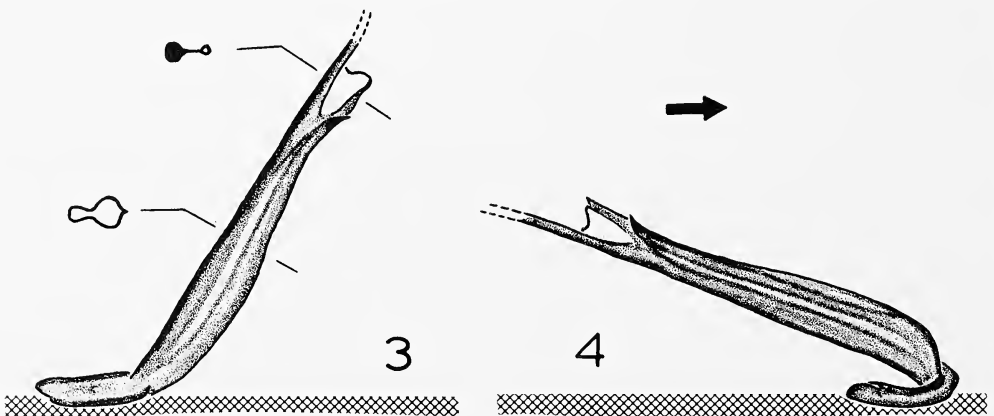
In the descriptions that follow, the orientation of the spermatophore is given with respect to the orientation of the male: 0° is parallel to the substrate, with the free, distal end directed anteriorly (pedicel posterior), while 180° is also parallel to the substrate, but with the free, distal end directed posteriorly.

SPERMATOPHORE FORM AND FUNCTION

Centruroides sculpturatus Ewing (Buthidae)

Figs. 3-4

Spermatophore flagelliform. Pedicel very flat, 1.2-1.4 mm long, 0.7-0.8 mm wide. Trunk 4.6-4.8 mm long, 0.2 mm wide, 0.6-0.7 mm deep (Fig. 3). Trunk with short, narrow, distal sperm tube opposite flagellum base, connected to it by a thin, partially



Figs. 3-4.—Spermatophore of *Centruroides sculpturatus* Ewing, from Maricopa Co., Arizona: 3, lateral aspect of pre-insemination spermatophore; 4, lateral view of post-insemination spermatophore. The flagellum is not shown. Arrow indicates direction faced by male.

sclerotized membrane. Sperm tube basally with paired, strongly sclerotized *subdistal hooks*. Flagellum subcircular in cross-section, diameter about 0.1 mm, length unknown.

During mating the male lowers himself to the substrate and attaches the pedicel. The body is then raised, pulling out the spermatophore trunk which forms an angle of 55° . At this stage the subdistal hooks are directed prolaterally (Fig. 3), and incapable of engaging the genital operculi of the female. The male retreats slowly backwards (pulling the female along), and throughout this backward motion the flagellum remains partially inside the genital opening of the male, pulling the trunk of the spermatophore and forcing it to bend over backwards at the pedal flexure (Fig. 4). Rotation of the trunk brings the subdistal hooks into an upward facing position favorable for insemination. Simultaneously the male pulls and guides the female over the spermatophore so that her genital operculi are eventually positioned above, or slightly beyond, the subdistal hooks. The male rocks the female so that her genital operculi engage the subdistal hooks, and are forced open, allowing the sperm tube of the spermatophore to be inserted into the genital opening. Continued rocking of the female by the male produces longitudinal compressional stresses on the trunk of the spermatophore, forcing sperm through the sperm duct and into the genital opening of the female.

Immediately after insemination the male releases the female and moves away, breaking the flagellum somewhere along its length (although the break usually occurs near the base). The post-insemination spermatophore does not spring back to its original position, but rather remains bent along the pedal flexure at an angle of about 160° (Fig. 4).

Didymocentrus comondae Stahnke (Diplocentridae)

Figs. 5-7

Spermatophore lamelliform. Pedicel 0.7-1.0 mm long, 0.4-0.5 mm wide. Pedal flexure very distinct. Trunk 1.4-1.5 mm long, subcircular in cross-section with median diameter 0.9-1.1 mm. Truncal flexure marked ventrally by sharp infolding, laterally by paired symmetrical inflections (representing most heavily sclerotized areas of spermatophore), and dorsally by broad median lobe projecting distally over sperm duct opening (Figs. 5-6). Capsule simple, consisting of symmetrically folded invagination (Fig. 7). Lamella 2.7-3.0 mm long, 0.3-0.4 mm wide, 0.5-0.6 mm deep; appears rather flexible terminally and curves downwards (Figs. 5, 7).

During mating the male attaches the pedicel to the substrate and slowly retreats backwards, expelling the entire spermatophore while pulling the female over it. The trunk of the pre-insemination spermatophore forms an angle of about 130° , and the lamella of about 140° (Fig. 5), and is already properly oriented for insemination with the sperm duct directed upward. As the female moves over the spermatophore, and her genital opening is above or slightly beyond it, the sharp (dorsal) edge of the lamella fits into the groove between her genital operculi. The male pushes the female backwards, and the lamella forces her genital operculi to open, guiding them into the respective lateral inflections of the truncal flexure. The backward thrust of the genital operculi on the spermatophore tends to bend the spermatophore forward along the pedal flexure. As this bending motion is initiated the lamella collides against the venter of the female, so that the spermatophore is folded upon itself. As the spermatophore is folded, the pedicel

exerts pressures upon the dorsal side of the trunk and the blunt (ventral) edge of the lamella exerts pressures upon the ventral side of the trunk, resulting in the eversion of the capsule and the ejection of the sperm mass into the exposed genital opening of the female.

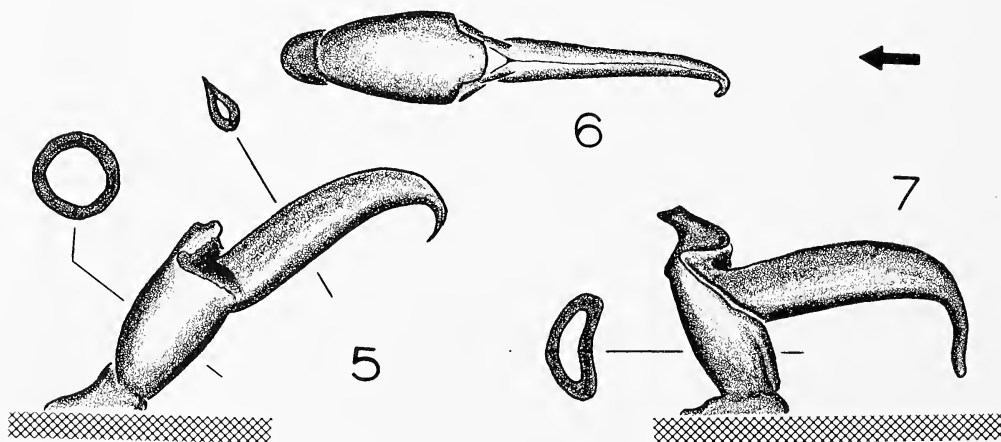
The post-insemination spermatophore does not resume its original position. The trunk, having been bent forward, now forms an angle of 70° ; the lamella, having been bent downward, forms an angle of 170° ; and the capsule remains in the everted position (Fig. 7).

Superstitionia donensis Stahnke (Chactidae)

Figs. 8-9

Spermatophore lamelliform. Pedicel 1.2 mm long, 0.6 mm wide. Trunk about 1.2 mm long, 0.6 mm wide, distally bearing paired small dorsal spiniform processes, medially directed, which project slightly over sperm duct opening (Fig. 9). Capsule absent. Lamella 1.8 mm long, width varies from 0.35 to 0.50 mm, depth from 0.30 to 0.40 mm; resembling "T" - beam in cross-section. Dorsal edge of lamella asymmetrically sigmoid in profile. Right and left halves (hemispermaphore lamellae) curl outwards ventrally, producing "T" - beam effect on lamella (Fig. 8). Curl extends ventrally from tip to base of lamella, across truncal flexure, ending dorsally in paired recurved hooks slightly distal to sperm duct opening (Fig. 9).

The pre-insemination spermatophore of *S. donensis* is unknown, and the events leading to insemination can not be reconstructed. In the post-insemination spermatophore the trunk forms an angle of about 130° , and the lamella of about 185° with the ventromedian edges of its two halves spread apart subdistally (Fig. 8). There appears to be no bending at the pedal flexure, and sperm ejection may be accomplished solely by bending along the truncal flexure.



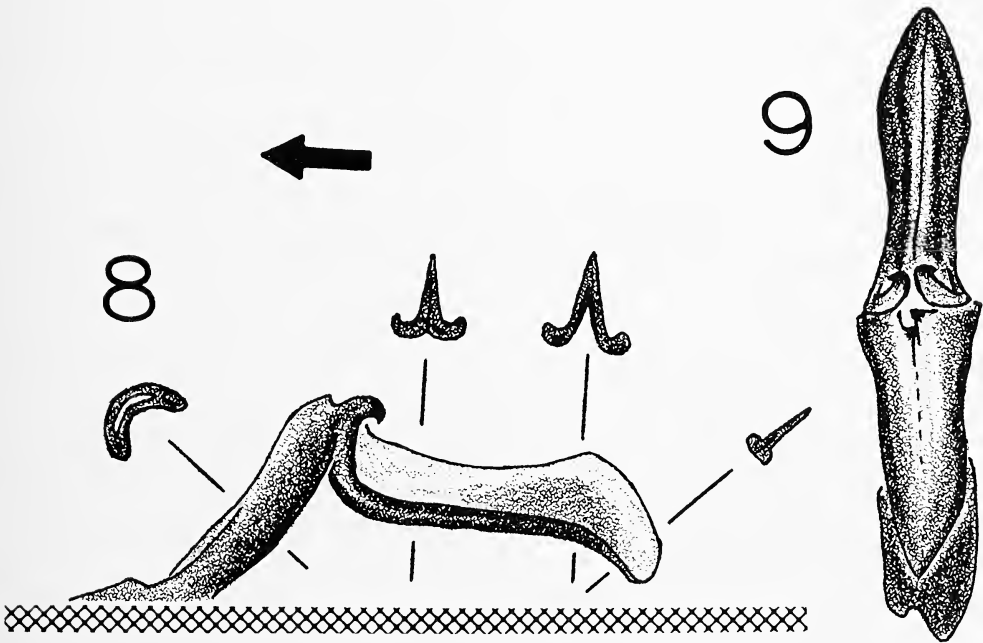
Figs. 5-7.—Spermatophore of *Didymocentrus comondae* (Stahnke), from Baja California Sur, Mexico: 5, lateral aspect of pre-insemination spermatophore; 6, dorsal aspect of pre-insemination spermatophore; 7, lateral aspect of post-insemination spermatophore. Arrow indicates direction faced by male.

Vaejovis confusus Stahnke (Vaejovidae)

Figs. 10-14

Spermatophore lamelliform. Pedicel 1.1-1.2 mm long, 0.8-1.1 mm wide. Pedal flexure well defined (Figs. 10, 11). Trunk 1.9-2.0 mm long, subcircular in cross-section with median diameter 1.1-1.2 mm (diameter increases distally to accomodate capsule). Truncal flexure marked ventrally by moderate transverse fold, laterally by paired symmetrical inflections, dorsally by capsule (Figs. 10, 11). Transverse ridges marking beginning of lateral inflections extend ventrally along blunt edge of the lamella, and dorsally along base of lamella for short distance before ending abruptly in paired, heavily sclerotized recurved hooks (Figs. 10, 13, 14). Lamella 3.5-3.8 mm long; cuneiform in cross-section, median width 0.20-0.25 mm, median depth 0.5-0.6 mm.

During mating the male attaches the pedicel to the substrate and backs away slowly, expelling the entire spermatophore. The trunk of the pre-insemination spermatophore forms an angle of about 130° , and the lamella of about 145° (Fig. 10), with the sperm duct opening directed upward. As the female moves over the spermatophore, the lamella fits into the groove between her genital operculi and acts as a guide. The female is rocked by the male, and during one of the backward strokes her genital operculi slide into the lateral inflections at the truncal flexure, forcing the operculi to open and engage the dorsal hooks of the spermatophore. Simultaneously the spermatophore bends along the pedal and truncal flexures (Figs. 13, 14), the capsule is everted along its basal hinge, and the sperm mass is ejected into the exposed genital opening of the female.



Figs. 8-9.—Post-insemination spermatophore of *Superstitionia donensis* Stahnke, from Cochise Co., Arizona: 8, lateral aspect; 9, dorsal aspect. Arrow indicates direction faced by male.

The post-insemination spermatophore remains somewhat folded upon itself, with the trunk forming an angle of about 90° , the lamella of about 180° , and the capsule remains everted.

Hadrurus arizonensis Ewing (Vaejovidae)

Figs. 15-16

Spermatophore lamelliform. Pedicel quite massive, 4.0-5.0 mm long, 2.2-2.6 mm wide. Pedal flexure very conspicuous. Trunk 4.0-5.0 mm long, 1.0-1.3 mm wide, 2.0-2.3 mm deep, deviating considerably from subcircular cross-sectional plan previously encountered. Trunk characterized anterodorsally by sharp longitudinal ridge along hemispermatophore-seam, posteroventrally by paired longitudinal flanges and median longitudinal depression (Fig. 15). Truncal flexure marked ventrally by feeble transverse fold, dorsally by sperm tube, laterally by two pairs of heavily sclerotized longitudinal ridges: mediolateral ridges straight, ending gradually along lamella; dorsolateral ridges curve distally, ending near sperm duct opening (Fig. 15). Lamella 4.0-4.5 mm long, 1.0-1.5 mm wide, 2.3-2.7 mm deep, with posteroventral edge weakly flanged.

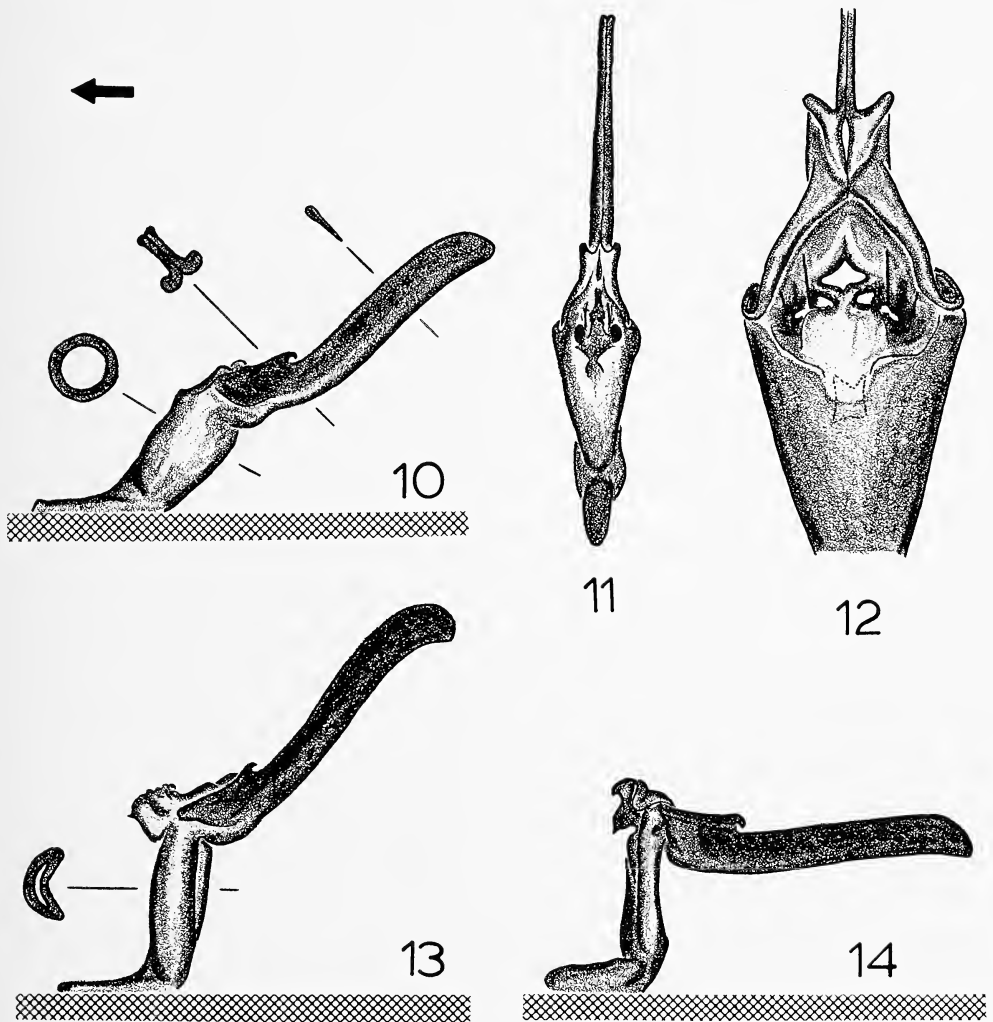
In the recently deposited spermatophore both trunk and lamella form an angle of about 150° . During mating the anterodorsal edge of the lamella functions as a guide in the same manner previously described for other lamelliform spermatophores. When the female is pushed backward her genital operculi slide into the grooves located between the paired ridges of the spermatophore, and continued backward pressure eventually forces the genital operculi to open and the spermatophore to bend along the pedal flexure. The lateral ridges of the spermatophore, however, apparently act as structural reinforcements that prevent bending at the truncal flexure. As the spermatophore bends forward along the pedal flexure, apparently the hemispermatophores become separated and spread apart along the ventral seam (Fig. 16). It is not known whether this change is brought about due only to the pedal flexure, or if a short-lived "truncal flexure" develops after the ventral seam of the spermatophore is spread apart. The necessity for a short-lived truncal flexure is suggested by the extent of the pedal flexure and by the orientation of the sperm duct opening in the post-insemination spermatophore. The formation of a pedal flexure, the spreading apart of the ventral seam of the spermatophore, and the formation of a short-lived truncal flexure (if one indeed occurs), are responsible for the ejection of the sperm mass into the genital opening of the female.

The post-insemination spermatophore of *H. arizonensis* displays a strong pedal flexure, the trunk and lamella form an angle of about 65° , and the sperm duct opening is oriented at 15° . The trunk resembles a horse-shoe in cross-section (Fig. 16) due to the opening of the ventral seam, has a width of about 1.3-1.5 mm and a depth of 2.3-2.7 mm. The lamella is roughly "V-shaped" in cross-section (Fig. 16) due to the opening of the ventral seam.

DISCUSSION

Indirect sperm transfer by means of spermatophores occurs in six Recent orders of arachnids: scorpions, pseudoscorpions, uropygids, schizomids, amblypygids, and acarines (Weygoldt 1975). Scorpion flagelliform spermatophores do not resemble, either morphologically or functionally, any other arachnid spermatophores. Scorpion lamelliform sper-

matophores, however, show strong morphological and functional similarities with those of atemnid pseudoscorpions (Cheliferoidea, Atemnidae). Although pseudoscorpion spermatophores are diverse (Weygoldt 1969, 1975), those of *Atemnus politus* (Simon) have: (a) a distinct pedicel and trunk connected by a well marked pedal flexure; (b) "paired, wing-like structures under the sperm package" (Weygoldt 1969:63) that closely resemble the lamella of scorpion spermatophores, and may be homologous to them; (c) a distinct truncal flexure and an eversible capsule; and (d) insemination apparently proceeds in a similar way to that described above for *Vaejovis confusus*, as suggested by examination of

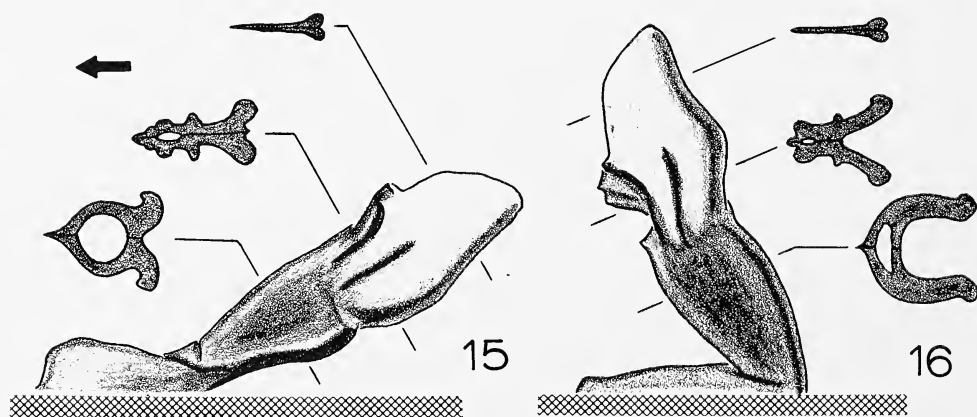


Figs. 10-14.—Spermatophore of *Vaejovis confusus* Stahnke, from Maricopa Co., Arizona: 10, lateral aspect of pre-insemination spermatophore; 11, dorsal aspect of pre-insemination spermatophore; 12, detail of dorsal aspect showing the infolded capsule; 13, lateral view of spermatophore during initial stages of insemination showing the partial eversion of the capsule; 14, lateral aspect of post-insemination spermatophore. Arrow indicates direction faced by male.

its pre-insemination and post-insemination states (Weygoldt 1969:63, fig. 57). The implications of this apparent homology in spermatophores of scorpions and pseudoscorpions with respect to their phylogenetic relationships and the classification of the Arachnida will be explored elsewhere.

The spermatophores of representatives of six of the seven currently recognized families of Recent scorpions are known. The family Buthidae is characterized by flagelliform spermatophores, and the families Bothriuridae, Chactidae, Diplocentridae, Scorpionidae and Vaejovidae by lamelliform spermatophores.

Pavlovsky (1924) studied the male genital apparatus of 28 genera of scorpions and found three distinct morphological types among them. The first type, which he called the complex type, is characterized by (a) the prolongation of the paraxial organs into a flagellum, (b) one cylindrical gland, (c) one oval gland, (d) two pairs of anterior accessory glands, and (e) a terminal dilation of the vas deferens. The complex type of male genital apparatus is found only in buthids, i.e., scorpions with flagelliform spermatophores. The second type, called by him the simple type, is characterized by the absence of: (a) a terminal flagellum on the paraxial organs, (b) cylindrical glands, (c) oval glands, (d) anterior accessory glands, and (e) the terminal dilation of the vas deferens. The simple type of male reproductive system occurs in the families Bothriuridae, Chactidae, Diplocentridae, Scorpionidae and Vaejovidae, i.e., those with lamelliform spermatophores. The third type, which Pavlovsky (1924) called the intermediate type, resembles the simple type but has one pair of anterior accessory glands. This type is found in *Chaerilus* (Chaerilidae) and *Calchas* (Chactidae, Calchinae). On the basis of the morphology of the male genital apparatus I believe that the spermatophore of *Chaerilus* and *Calchas* will probably not be flagelliform, but rather should be lamelliform or of an undescribed form approaching it. This prediction is indirectly supported by information available regarding the female reproductive systems in scorpions (Pavlovsky 1925). In buthids the ovariterus is a reticular mesh with eight "cells" (ten anastomoses), and in the other families (including *Chaerilus*) it is a reticular mesh with six "cells" (eight anastomoses). Thus, the



Figs. 15-16.—Spermatophore of *Hadrurus arizonensis* Ewing, from Maricopa Co., Arizona: 15, lateral aspect of pre-insemination spermatophore; 16, lateral aspect of post-insemination spermatophore. Arrow indicates direction faced by male.

Chaerilidae appear to be more closely related to those scorpions with lamelliform spermatophores than they are to those with flagelliform spermatophores. The significance of these findings regarding the phylogeny and classification of the order will be discussed in a future contribution.

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The spermatophores of *D. comondae* were collected by Mr. Joseph L. Bigelow, whom I thank for the gift. The spermatophore of *S. donensis* was obtained by Mr. Vincent D. Roth and is deposited in the collection of the American Museum of Natural History; I thank Dr. Norman I. Platnick of that institution for allowing me to study it. Finally, the spermatophores of *C. sculpturatus*, *V. confusus*, and *H. arizonensis* were obtained from Dr. Eric Toolson, who should be credited with the spermatophore-recovery procedure described above, and to whom I am very grateful for his cooperation. Drafts of the manuscript were read by the following friends and colleagues, to whom I am most thankful: Mr. James C. Cokendolpher, Dr. David E. Foster, Dr. Willis J. Gertsch, Dr. Herbert W. Levi, Dr. Robert W. Mitchell, Dr. Norman I. Platnick, Mr. Michael E. Soleglad, Mr. Frederick W. Wagner, and Dr. Stanley C. Williams.

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BEHAVIOR AND ECOLOGY OF MATING IN THE CANNIBALISTIC SCORPION, *PARUROCTONUS MESAENSIS* STAHNKE (SCORPIONIDA: VAEJOVIDAE)

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ABSTRACT

During the seasonal mating period, mature males undergo alteration in behavior and ecology; they are more vagrant and feed less than all other components of the population.

Cannibalism of mature males by mature females combined with other factors related to mating contribute to a higher death rate of adult males as compared to adult females.

Reproductive behavior consists of mating rituals which minimize predatory behavior and elicit the cooperation necessary for indirect sperm transfer. These rituals include the *promenade à deux*, cheliceral massage, post-mating escape and heretofore undescribed behavior which precedes the actual mating dance.

INTRODUCTION

Mating behavior is often complicated by conflicting stimuli which simultaneously produce the incompatible tendencies to flee, attack and mate (Tinbergen 1953, Morris 1956). Agonistic and escape behaviors must be inhibited so partners can obtain sufficient proximity for transfer of sperm. This is often accomplished during courtship where a stereotyped series of cues allows recognition of potential mates and produces a non-aggressive interaction with sufficient coordination and cooperation for successful fertilization (Bastock 1967, Morris 1970). To understand how the behavioral requisites for mating are achieved, courtship can be analyzed through an ethogram of its component behaviors. Such analysis may also reveal species-specific mechanisms which inhibit genetic introgression by closely related species (Mayr 1963).

Scorpions have many characteristics which suit them well for this type of behavioral analysis: since they fluoresce under ultraviolet light (Stahnke 1972) they are easily detected and observed in the field at night; they are faunistically diverse and abundant in desert habitats (Polis and Farley, in press); they are often cannibalistic (see Table 1); and they have an elaborate courtship (Alexander 1956, 1957, 1959).

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Scorpion courtship and mating have been described for many species (Tables 1 and 2; Garnier and Stockman 1972). However, it is not clear in those accounts how recognition of sexual partners occurs or how aggressive and escape behaviors are sufficiently inhibited so mating can be completed.

The purpose of the present study is to analyze the relationship between mating behavior and cannibalism of mature males by mature females. Our data show that adult females normally feed upon adult males even in the breeding season. Courtship consists of a sequence of behaviors which apparently function to decrease predation and elicit the cooperation and coordination necessary for indirect sperm transfer. The breeding season is characterized by marked changes in the behavior and ecology of mature males which decrease male survivorship and increase the probability that these males will be cannibalized. This is the first account of courtship for a member of the family Vaejovidae. All data in this paper are from the field.

METHODS

This study was conducted at a sand dune adjacent to state Highway 111 about 9 km northwest of Palm Springs in Riverside County, California. It is at 33° 54' N, 166° 37' W, at an elevation of 320 m. Located at the foot of Mount San Jacinto (elevation 3,300 m), the dune is in the northwest extreme of the Colorado Desert. This area is subject to seasonally high diurnal temperatures, low relative humidity, and low annual precipitation (average = 13.30 cm) (Edney 1974, U.S. Environmental Data Service 1975). In suitable habitats, this species occurs at very high densities. In the study area, maximum density of scorpions active on the surface was over 1500/hectare while maximum total densities estimated from marked animals exceeded 3000/hectare (Polis in prep).

The entire study area was about 75 hectares. Within this area a grid 28 by 50 m was constructed by placing marker stakes 2 m apart in 15 longitudinal rows. Each row was separated by 2 m. Portable lights (Coleman Charger 3000 and Burgess safari-light) with ultraviolet bulbs (Sylvania F8T5) were used to locate scorpions. All data were gathered from May 1973 through September 1977 during 900 field hours on over 225 different nights. In the four years of this study, over 850 scorpions observed in the grid were individually color coded. Unique markings were achieved by using fluorescent paints of different colors in various dot combinations. Individual burrows were marked with coded stakes. Individual activity, forage range from burrow, and the distance scorpions moved between successive sightings were tabulated from repetitive surveys of the grid area. Grid surveys were conducted on the average of once per week for the entire research period. Data from the first sighting of scorpions after marking were never used as the markings may have disturbed the animals enough to cause changes in behavior or ecology. However, such changes were rarely observed.

Data obtained by surveying the entire study area include sex and age structure, mating observations, feedings, cannibalism and percent of individuals moving when first observed. Data on diet and cannibalism were readily obtained since scorpions digest their prey externally in a process which often lasts several hours.

Field data were recorded on a pocket tape recorder and were transcribed later. By using the tape recorder, data were usually gathered without using white light. Photographic records were obtained using an electronic strobe and macro lens. Distances were usually measured, but to avoid disturbance during matings, distances were estimated to

the nearest 5 cm (if greater than 15 cm) or to the nearest 2 cm (if less than 15 cm). All scorpion lengths were standardized according to Stahnke (1970) and were measured from anterior edge of prosoma to the end of the last metasomal segment.

RESULTS

Cannibalism as a Mortality Factor.—The scorpion, *Paruroctonus mesaensis* Stahnke, is a facultative raptorial predator which primarily uses substrate vibrations to locate prey (Brownell 1977a and 1977b). The direction of objects moving on or just beneath the substrate can be determined at distances up to 50 cm. The scorpion turns abruptly towards the source of the substrate disturbance, advances and seizes the object with its pedipalps. Any moving object in the proper size range is attacked without apparent discrimination.

This foraging behavior explains the high rate of cannibalism exhibited by this species. Conspecific individuals constitute 9.10 percent of the diet ($n=792$). This was the fourth most commonly observed prey item. Further, 17.1 percent of all cannibalisms consisted of mature females preying on mature males during the breeding season.

Cannibalism of mature males apparently has a significant effect on demography and age distribution (Polis, in preparation). Males generally do not live past their first breeding season. The average survivorship of mature males from one breeding season to the following is significantly lower than for mature females. Of 145 mature males marked during the summers of 1973, 1974, and 1975, only 5.8 percent were observed to be present the next spring. By contrast, the survivorship of marked mature females ($n=169$) was 18.9 percent.

Annually, most males are newly matured virgins. At the start of the breeding season in late spring 1975 and 1976, only 18.2 percent of the mature males ($n=121$ scored) were mature the previous year. At this time, overwintering mature animals of both sexes are readily distinguished from newly matured virgins by differences in length and weight. By the end of the breeding season, individuals that reached maturity that season constituted the great majority of mature males. By comparison, 62.7 percent of the mature females ($n=186$ scored) were mature the previous season. The oldest marked male observed was only 37 months, while the oldest marked female was at least 58 months.

In *P. mesaensis*, the behavior associated with cannibalism is stereotyped and has some components not present during attack on insect prey. In the six instances in which we observed the onset of a cannibalistic attack, the attacked individual was moving. On being seized, the attacked scorpion flicks its metasoma at its attacker in an attempt to sting. Almost immediately, each scorpion grabs the other scorpion's metasoma with one chela. The other chela is used to grasp another part of the adversary's body. No individual was observed to attack a larger moving scorpion.

Behavior During the Mating Season.—Matings were observed in the field as early as 26 May (1976 and 1977) and as late as 2 October (1975), but 80 percent of the observed matings occurred in August and September (distribution of matings by month in percent: May—10; June—5; July—0; August—50; September—30; October—5). Of all matings recorded, 95 percent occurred on nights of new moon or when the moon was not present.

During the mating season, the behavior of adult males is substantially altered. They become skittish and strike with the slightest provocation, and they appear to feed less than mature females. In 1974, 1975, and 1976, males represented 35.5 percent of the total

adult population (n=1197 scored). However, adult males feeding at the time of observation constituted only 32.1 percent of the total number of adults (n=209) observed feedings.

Adult males also become vagrant (Fig. 1) during the mating season and abandon their burrows nightly. The average distance between successive sightings (on different nights) of marked mature male scorpions was 34.7 m (Table 3). Some marked individuals were observed to travel more than 100 m in a night and over 23 m in one-half hour. Further, 48.3 percent of all mature males were moving at the moment of first sighting.

This is in marked contrast to the rest of the population. Normally, mature females, immature scorpions of both sexes and adult males not in the breeding season forage a short distance from their burrows. Marked mature females (n=168) were observed (mean \pm S.D.) 0.9 ± 1.1 m from their marked burrows. The average distance between successive sightings (on different nights) of marked mature female scorpions was 4.0 m. This value is significantly different from the of mature males. Mature females, immature animals and mature males out of the breeding season are normally sedentary. Only 1.8 percent of females and immatures were moving at the moment of observation. Only 5.2

Table 2.—Scorpion species for which courtship have been studied. Roman numbers and letters correspond to families and species respectively in Table 1.

TAXON	REFERENCE
I—Bothriuridae	
a) <i>Bothriurus bonariensis</i> (Koch)	de Zolessi 1956, Varela 1961
b) <i>B. asper araguayae</i> (Pocock)	Matthiesen 1968
c) <i>Urophonius brachycentrus</i> (Thorell)	Maury 1968
II—Buthidae	
d) <i>Buthus occitanus</i> Amoreux	Fabre 1923, Auber 1963
e) <i>Tityus trivittatus</i> Lutz and Mello	Bücherl 1956
<i>Tityus bahiensis</i> (Perty)	Bücherl 1956
f) <i>Leiurus quinquestriatus</i> (H. et E.)	Thorton 1956, Shulov and Amitai 1958, Abushama 1968
g) <i>Buthotus judaicus</i> Simon	Shulov and Amitai 1958
h) <i>Parabuthus planicauda</i> (Pocock)	Alexander 1959
<i>Tityus trinitatis</i> (Pocock)	Alexander 1959
i) <i>Centruroides insulanus</i> (Thorell)	Baerg 1961
j) <i>Centruroides vittatus</i> (Say)	McAlister 1965
k) <i>Isometrus maculatus</i> (De Geer)	Probst 1972
l) <i>Androctonus australis</i> (L.)	Auber-Thomay 1974
III—Chactidae	
m) <i>Euscorpheus italicus</i> Herbst	Angermann 1955, 1957
<i>Euscorpheus flavicaudis</i> De Geer	Angermann 1955, 1957
<i>Euscorpheus carpathicus</i> (L.)	Angermann 1955, 1957
IV—Diplocentridae	
n) <i>Nebo hierichonticus</i> (Simon)	Shulov and Amitai 1958, Rosin and Shulov 1963
V—Scorpionidae	
o) <i>Urodacus abruptus</i> Pocock	Southcott 1955, Smith 1966
p) <i>Opisthophthalmus latimanus</i> (Koch)	Alexander 1956, 1957, 1959
q) <i>Heterometrus scaber</i> Koch	Mathew 1957
r) <i>Pandinus imperator</i> Koch	Garnier and Stockman 1972
VI—Vaejovidae	
s) <i>Paruroctonus mesaensis</i> Stahnke	Present study
t) <i>Paruroctonus borregoensis</i> Williams	Present study

percent of mature males out of the breeding season were observed moving. These values are significantly different from the percentages obtained for males in the breeding season.

In the study area, males of four sympatric scorpions (*Paruroctonus borregoensis* Williams, *Hadrurus arizonensis* Ewing, *Vaejovis confusus* Stahnke and *V. puritanus* Gertsch), were also observed to be vagrant during spring and summer. A large percentage of males of these species were moving when first observed while females and immature animals were generally stationary.

Courtship and Mating.—*Promenade à deux* and spermatophore deposition were observed in the field on twenty occasions. Pre-promenade behavior was observed on three occasions. In all cases notes were taken. Photographic records were obtained from four matings.

The mating described below and depicted in Fig. 2 occurred 11 August 1975 between a male, 1.72 g and 70 mm long and a female, 2.71 g and 74 mm long. Parenthetical Roman numerals correlate the text with Fig. 2. The moving male was first observed about 7 m from the stationary female. Its movement took it to within 30 cm of the female. The male exhibited no apparent awareness of the female and began to move away. Quite rapidly, however, the female moved to the male, grasped and released the male's body with her chelae, clubbed or attempted to sting him with her metasoma, and then retreated (Fig. 2, I). We call this the female's "mating attack behavior". Clubbing is defined as hitting with the metasoma while the sting is tucked away (McAlister 1966). The male then began to "strut defensively" (Stahnke 1966). During this behavior, the male stilts on his legs, his metasoma is raised perpendicular to the ground, and he remains still or moves intermittently while his pectines slowly sweep the substrate. This behavior is common after disturbance or attack.

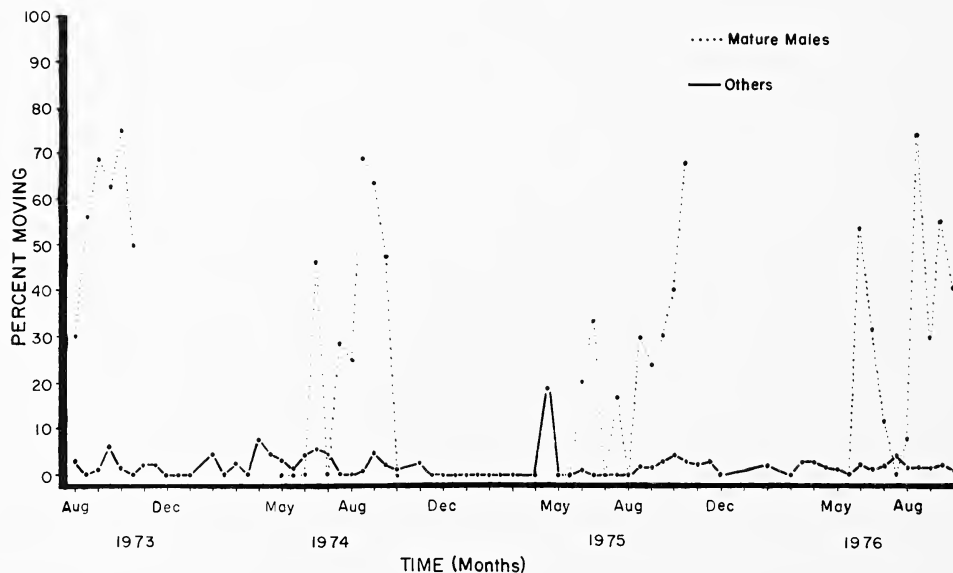


Fig. 1.—Percent animals moving at moment of first sighting. Mature males were not present on the surface during the winter months. Data taken from observation of 334 mature males and 4,348 mature females and immature animals.

After several minutes, the male ceased to strut and began to move normally. The female repeated her attack behavior (II). The male responded as before. After strutting a short time, the male “juddered” (Alexander 1957). Juddering consists of rapid rocking or shaking of the body back and forth on immobile legs. The pectines are spread out during this behavior. The male then began to move haltingly. The female advanced and grasped the male with her chelae but did not club or attempt to sting (III). The male turned, raised his metasoma, but he also did not club or attempt to sting. The male then strutted and juddered but the strutting time was relatively short and neither the body nor the metasoma were raised as highly as previously. The female again advanced to the male as in the third encounter (IV), but this time the male did not strut. He juddered twice. In the fifth encounter (V), the female gently touched the male on his chelae before she retreated a short distance. The male turned lightly and appeared to search for the female. His pectines were spread and occasionally swept the substrate.

Whereas prior to this time the female had made advances and the male responded, now the male seemed to take the initiative. He advanced and contacted the intermittently-moving female (VI). He touched the female for about 30 seconds by simultaneously grasping the base of the female’s metasoma and the base of her right pedipalp. He released the female, retreated a short distance and juddered (VII). The female then moved to the male and grasped his left chelae with her right chelae. She soon released him and retreated 2 cm. The male juddered again before contacting the female. They remained motionless for 15 seconds before beginning the *promenade à deux* (VIII). The promenade (Fabre 1923) is the “mating dance” during which the male grasps the female’s chelae with his own; the male then leads the female as the pair moves together. The promenade began 22 minutes after the initial contact. They moved together about 25 cm before the male released his grasp of the female for a short period. The male juddered before reinitiating the promenade.

During the promenade, several behaviors occurred. The male’s pectines were widely spread and sporadically swept the substrate. The male generally traveled directly backwards. Commonly, the male alternately pulled more strongly on one than the other of the female’s pedipalps as they traveled. On four occasions, the female actively resisted movement. The female was generally dragged forward at these times although once she moved backwards and pulled the male forward a short distance. Each time the female resisted,

Table 3.—Vagility of mature males during the breeding season compared to other components of the population. On the average, mature males move further between successive sightings on different nights as compared to mature females. Mature males during the breeding season are more frequently observed to be moving at the time of first observation than all other components of the population. Distance moved represents mean and standard deviation. The Z statistic to test differences in means and differences in proportions was used to establish significance. (n=sample size; p=probability).

	Distance from last sighting (m)	n	Z	p
Marked mature males during breeding season	34.7±24.9	44		
Marked mature females during breeding season	4.0± 8.7	177	3.0	.001
	Percent moving	n	Z	p
Mature males during the breeding season	48.3	315		
Mature males out of the breeding season	5.2	19	3.6	.0001
Mature females and all immature scorpions	1.8	4,348	36.5	<.0001

the male initiated "cheliceral massage" ("kissing", Southcott 1955). During this behavior, the male grasps and kneads with his chelicerae the female's chelicerae, prosomal edge, and/or the articulation of the pedipalps.

The promenade lasted 9.25 minutes before the initiation of spermatophore deposition. The pair traveled approximately 8 m during this time. The male encountered a twig 6 mm in diameter and 15 cm long (IX). The body axis of the male was perpendicular to the long axis of the stick. He backed up until his genital segment was directly over the stick. He showed several behaviors during this time and before deposition of the spermatophore: cheliceral massage was almost continual; he juddered on two occasions; his metasoma was curled so far forward that it touched the base of the female's pedipalp; his pectines were actively sweeping; and his second and third pair of legs moved sporadically in the sand, actually producing grooves ("sand scraping", Alexander 1959). The male's genital aperture was adressed against the stick while the spermatophore was extruded and secured to the stick (IX).

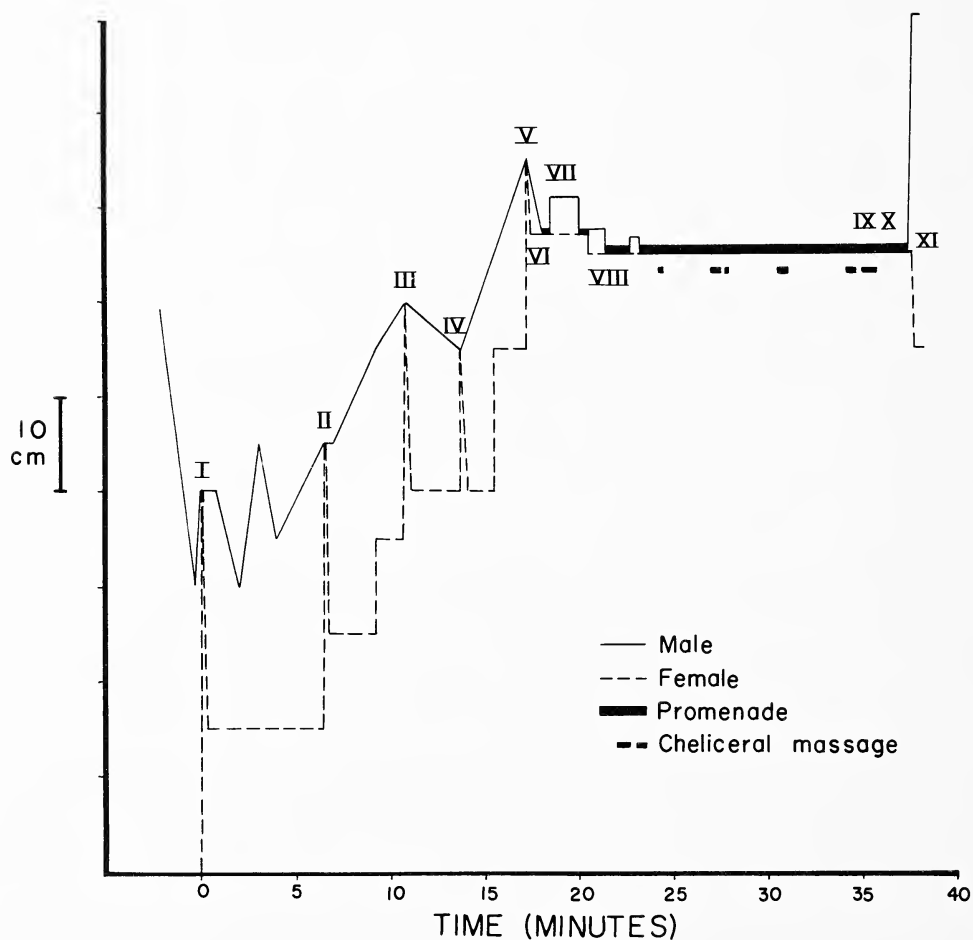


Fig. 2.—Interaction and spatial relationship of male and female during courtship and mating behavior. The ordinate indicates movement of either male or female relative to each other but not movement of the pair together during the promenade. Roman numerals correlate with descriptions of behavior in text.

The male then pulled the female over the spermatophore. They moved back and forth over the stick three times before the female exhibited "head-stand behavior." During this behavior, the female stilted her mesosoma while she pressed her genital region close to the stick. The spermatophore remained on the stick while the sperm was presumably transferred. Both scorpions remained motionless for a short time before the male exhibited "escape behavior." He quickly and repeatedly probed the female's mesosoma with his sting while concurrently disengaging his grasp. We could not determine if the male stung the female. He then ran off about 25 cm (XI). The female slowly moved a short distance before stopping. She then began "swaying" for about 45 seconds. During swaying the female raised her body above the ground while moving side to side on her immobile legs. Finally, the female began to move away. The male remained motionless. From the first encounter to the end of the swaying, the entire mating lasted 38.5 minutes.

Slight variations of these basic mating behaviors were observed in other matings. In the other two observations of pre-promenade behavior, the initial forays by the female during mating attack behavior were at distances of 20 and 25 cm. One of the mating attack behaviors by the female consisted of a series of three encounters while the other was of four encounters.

During the promenade, the male occasionally leads the female by only one chela. This is most common when the pair must execute a sharp turn to avoid an obstacle. Once during a promenade, the male released the female. Then, perpendicular to the long axis of the female's body, the male seized the base of her pedipalp and her metasoma. This lasted about 30 seconds before the promenade was resumed.

During headstand behavior, we observed that the female's genital operculum opens during her headstand and makes contact with the apex of the spermatophore. This contact, resulting in insemination, lasts only 3 to 5 seconds.

Variations also were observed in escape behavior. The male either probes the female with his sting (five to fifteen times) or bats the female with his metasoma (two to five times). This disengagement process is usually rapid, lasting only 3 to 10 seconds. On three occasions, the female chased the male for a short distance; in most cases the female remained motionless or moved slowly.

Courtship from first observation of promenade through end of swaying was observed to last between 5 and 35 minutes. The distances traveled ranged from under 3 m to over 25 m. In 18 of 20 matings, spermatophores were deposited on sticks from 5 to 8 mm in diameter. Spermatophores were once deposited on a piece of sheet metal and once on the sand. The spermatophores remained fixed to all substrates except the sand. After deposition on the sand, the entire spermatophore was later found between the female's genital plates.

One mating of the congeneric species, *P. borregoensis*, was also observed in the field. This occurred on 2 October 1975 between a male (31 mm long, 0.37 g) and a female (35 mm long, 0.50 g). Most components of mating behavior were quite similar to those of *P. mesaensis*. The promenade was in progress when the pair was discovered. The following behaviors were observed: *promenade à deux* with chelae grasp; cheliceral massage following female resistance; the male's pectines actively sweeping the substrate; male juddering, sand scrapping, and cheliceral massage during spermatophore deposition; female headstand at the time of sperm transfer; male escape behavior, and female swaying. The male was unable to free himself from the female for a few seconds after he initiated escape behavior. Further, the female chased the male for a distance of about 15

cm before the male escaped. The promenade and mating lasted about 5 minutes. They traveled 0.8 m. The spermatophore was deposited on a stick 7 mm in diameter and 10 cm long.

DISCUSSION

The data show that cannibalism of mature males by mature females during the breeding season contributes to a higher death rate of adult males as contrasted to adult females. For mating to occur, there must be a reduction of these predatory tendencies and this appears to be accomplished in the courtship ritual by a series of brief but aggressive contacts which gradually increase in duration but decrease in violence.

Table 1 summarizes the mating behavior reported for scorpions. Mate cannibalism is common among scorpions and occurs within almost all other orders of archnids (Cloudsley-Thompson 1968). In spiders, as in scorpions, mate cannibalism occurs frequently and males often do not live more than one mating season (Bristowe 1941, 1958).

Intraspecific predation on mature male scorpions by mature females occur both during or directly after mating and during activity not associated with mating. There are several reasons why mature males are so vulnerable to cannibalism. On the average, mature males are significantly smaller than mature females (Polis and Farley 1979) and are within the normal size range of prey eaten by mature females (Polis in prep.). This dimorphism is important since, in all cases of cannibalism observed in the field ($n=76$), the prey was smaller than the predator. In 68.4 percent of 19 matings for which the participants were measured, the male was smaller than the female.

Further, when mature males move during the breeding season they produce substrate vibrations which are sensed by non-receptive (gravid or previously inseminated) females which appear to interpret moving males as potential prey. Finally, we observed cannibalism after mating on two occasions. In both cases the spermatophore was present on a stick and the female was eating the male.

Cannibalism is only partially responsible for the marked differential mortality of mature males compared with mature females. Other factors, related to breeding, may also contribute to male mortality: greater risk of predation during nightly movement; possibility of migration out of the habitat to less optimal areas; increased risk of heat death in shallow burrows which must be constructed nightly; greater energetic costs produced by movement and nightly burrowing; decreased foraging time and food intake as activity is devoted to reproduction rather than hunting; and increased probability of overwintering mortality due to inadequate food reserves. We have evidence from the field that moving males were attacked and eaten by vertebrate predators (Grasshopper mouse, *Onychomys torridus* (Wied-Neuwied) and owls). Male scorpions were observed while moving in adjacent habitats which do not support populations of *P. mesaensis*. In summer at dawn we have witnessed several males rapidly digging in freshly excavated shallow burrows.

It is probable that mature males of all vaejovid species become vagrant during the mating season. Males of the scorpions *Hadrurus* sp. (Williams 1970), *Anuroctonus phaiodactylus* (Wood) (Williams 1966), and *Paruroctonus boreus* (Girard) (Tourtlotte 1974) are nomadic during the breeding months. Analyses of can trap data (Gertsch and Allred 1965, Hibner 1971) almost always indicate a severe trap bias for mature vaejovid

males. This bias is probably a result of male movement during the breeding season (Allred 1973). Mature males of the scorpion *Urodacus abruptus* Pocock, in the family Scorpioniade, are more mobile than mature females (Smith 1966). Male vagrancy at this time may well be the main cause of gene flow among populations.

Female initiation of courtship has been reported in other scorpion species (Table I). Although he did not describe the mating, Bacon (1972) stated that females of the vaejovid scorpion, *Uroctonus mordax* Thorell initiate courtship. However, female mating attack has not previously been described. In female *P. mesaensis* this behavior is different from cannibalistic attack behavior; this suggests that she is in a receptive state prior to mating attack or the adult male triggers a less violent attack. During mating attack, the female does not secure a hold on the male's body. She retreats after each contact with the male, and she continues her forays to the male.

Substrate vibrations may be employed to identify potential mates and reduce violent interaction. Although mate recognition by information received through vibrations has not been reported in scorpions, it does occur in other organisms: many spider families (Bristowe 1941, 1958), fiddler crabs (Salmon 1965), Orthoptera (Frings and Frings 1958), and mosquitoes (Frings and Frings 1958). Intraspecific communication via substrate vibrations is also reported for eight orders of insects (Frings and Frings 1958; Autrum 1963; Dumortier 1963; and Alexander 1967) and for many species of mammals (Tembrock 1963).

In spiders, the primary sense used for prey detection is often also used for mate recognition (Bristowe 1941, 1958). In spiders that utilize vibration to detect prey, the female recognizes the male via male-specific vibrations.

The promenade provides the male and female scorpion with the mobility and coordination necessary to find a suitable substrate on which to deposit the spermatophore. Duration of the courtship seems to be primarily determined by the length of time it takes to find a solid surface for the spermatophore (Alexander 1957, 1959; Shulov and Amitai 1958; Rosin and Shulov 1963). The male's pectines sweep the surface during the entire promenade and become very active upon encounter with the proper substrate. Our observations support Carthy's (1966, 1968) contention that the pectines are used in discriminating surface texture. The dimorphic use of the pectines by the male during mating implies that the pectines may be an important structure in courtship and sperm transfer. Using morphometric analysis of growth, we have shown (Polis and Farley 1979) that the pectines are sexually dimorphic and exhibit growth characteristics of a masculine secondary sexual characteristic.

Cheliceral massage was only observed during the promenade when the female ceased moving and during spermatophore deposit and uptake. In both cases, the female appeared to become more docile and cooperative, suggesting that this behavior may function to suppress female predatory tendencies during the mating process.

Headstand and swaying behaviors probably serve mechanical functions. Headstand behavior is displayed only when the female is over the spermatophore. As the female's genital aperture dilates at this time, headstand behavior is associated with sperm uptake. Swaying may cause the sperm to travel further into the female's reproductive tract. Both of these previously unnamed behaviors have analogies in other families of scorpions (Table 1).

Male post-nuptial behavior reduces the probability of cannibalism by the female. After insemination, the female's reproductive tendencies may decrease while her cannibalistic

tendencies increase. Alexander (1959) reported that the female is always more aggressive after mating and must be avoided by the male. Escape behavior decreases the incidence of cannibalism by removing the male from the immediate proximity of the larger female. Both male escape behavior and mate cannibalism are widespread among scorpions (Table 1).

Table 1 allows a comparison of mating behaviors between vaejovids and other scorpion families. Only two behaviors, promenade with chelae grip and male pectine movement, have been observed in the five other families reported in the literature. Behaviors exhibited by *P. mesaensis* and reported in at least three of the other five families include juddering, cheliceral massage, sand scraping, and mate cannibalism by the female. Behaviors which are shared with only one or two of the other five families include male movement, female initiation, clubbing, headstand and swaying. Accidental and male initiation, promenade with cheliceral grip, female post-mating escape, and consumption of the spermatophore are behaviors exhibited by members of other families but which are not observed in the present study.

Female mating attack and subsequent male response have not been reported previously. As our work was conducted exclusively in the field, it is possible that these behaviors (and male movement) are merely heretofore undescribed. It is our experience that scorpions are much less active and aggressive in the laboratory than in the field. These pre-promenade behaviors may be suppressed in the laboratory and the numerous reports of matings initiated by males (Table 1) may be a laboratory artifact.

SUMMARY

During the breeding season, adult males are eaten by adult females during or after mating and by simple predation. Approximately 10 percent of the diet is individuals of the same species. Cannibalism of mature males combined with other factors related to breeding contribute to a higher death rate of adult males than of adult females.

Mating is seasonal. During the breeding season, mature males undergo alteration in behavior and ecology; they roam more and feed less than all other components of the population. This increased vagility of the male increases the chances they will be cannibalized, since these scorpions use substrate vibrations to locate prey.

Courtship is discussed in terms of mating behaviors which reduce predatory tendencies and elicit the pair coordination necessary for indirect sperm transfer. The behaviors include the *promenade à deux*, cheliceral massage, post-mating escape by the male and heretofore undescribed behavior which precedes the actual mating dance. Brief but aggressive contacts gradually increase in duration but decrease in violence before the mating dance begins. Indirect sperm transfer is also described.

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NESTS OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE): CHARACTERISTICS, PATTERN OF OCCUPATION, AND FUNCTION

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ABSTRACT

Phidippus johnsoni constructs tubular nests from silk under rocks, under pieces of wood, inside hollow reeds, etc.; and these are involved in molting, courtship, mating, oviposition, and other aspects of the spider's life history. Relatively large rocks and pieces of wood tend to be chosen for nest sites. Nest length tends to be two to three times greater than the spider's body length. Nests vary in shape, density, raggedness, and the degree to which they are cluttered with debris. Most spiders reside in nests of greater density and lesser raggedness and clutter. Molting and oviposition occur in especially dense nests. Spiders tend to remain inside nests for six days preceding and two days following molting. Spiders enter their nests before dark and remain inside at night. Much time is probably spent spinning. Males are more likely to be found outside nests compared to females and immatures, and the nests they occupy tend to be less dense. Marked spiders in the field employ the same nest sites for prolonged periods (maximum, 28 to 33 days), sometimes making excursions of as far as 1.2 m away from nests before returning. Two adult females in individual terraria each occupied a single nest for 6 to 7 months, sometimes making excursions of as far as 80 cm. Females in nature and the laboratory oviposited repeated batches in single nests. Sometimes nests built by other individuals were employed by spiders.

INTRODUCTION

Although prey capturing devices, such as the "nets" of dinopids, the "purses" of *Atypus*, and especially the "webs" of diverse species of spiders (see, e. g., Levi 1978, Risch 1977, Stern and Kullmann 1975, Witt *et al.* 1968) have received considerable attention, the silken structures of vagabond spiders have received relatively little attention. This paper will deal with the silk nests of *Phidippus johnsoni* Peckham and Peckham, a common salticid species in western North America. The range of this species is from the Great Plains to the Pacific Ocean and from Canada to Mexico, where it occurs in a variety of types of habitats from sea level to timberline.

Possessing one of the most highly developed invertebrate visual systems (Land 1972), the salticids are diurnal predators that use vision to stalk their prey (Gardner 1965). Although silk is not usually employed in prey capture, it plays a role in other aspects of the life of these spiders. The salticids build silken nests (retreats) inside which they molt,

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oviposit, and remain at night and during inclement weather. Also, nests are important in understanding the mating tactics of *P. johnsoni* and probably other salticids (Jackson 1977a, b). A male *P. johnsoni* encountering a female outside her nest employs a type of courtship comprised of vision-dependent displays. However, if the female is inside her nest, the male employs a non-vision-dependent, vibratory courtship. If the female is a subadult inside her nest, the male employs a third tactic involving the construction of a second chamber on the female's nest and cohabitation until she matures. Following each of the latter two tactics, mating takes place inside the nest.

General aspects of the life history of this species have been discussed elsewhere (Jackson 1978). The goal of this paper is to record the characteristics of nests and to investigate specific aspects of life history related to the use of nests by the spiders. Certain information from the life history study will be summarized here, since it will be important for the discussion of specific items in the text. In the laboratory, *P. johnsoni* undergoes 5 to 8 molts before reaching maturity. Adults tend to be approximately 10 mm in body length; males are smaller than females, maturing earlier and after fewer molts. Mature individuals do not molt further, and adults tend to survive 3 to 4 months. Females are iteroparous, ovipositing up to 5 successive batches of fertile eggs after a single copulation. Approximately one month passes between mating and the first oviposition, and the inter-oviposition interval for later batches is approximately one month. Eggs hatch nearly 3 weeks after oviposition. The postembryos remain inside the nest, and the first instar spiderlings tend to disperse from the nest 3 weeks after hatching occurs.

METHODS

General—Data concerning nests were gathered in the laboratory during the course of rearing a set of spiderlings from egg to adult (Jackson, 1978). Data from the field were gathered during censuses (Jackson, 1978) in which each nest in the census area was recorded. The census areas were at Tilden and Mt. Diablo in the Coastal Range, Pt. Reyes and Inglebrook at sea level next to the Pacific Ocean, Pothole Dome in the Sierra Nevada, and Whiskey Mountain in the Rocky Mountains. Whiskey Mountain is in Wyoming, and the other sites are in California.

The temperature in the laboratory was maintained at $24 \pm 1^{\circ}\text{C}$, the light regime was 11L: 13D (lights on, 0900 hrs.; off, 2000 hrs.) for spiders reared from eggs. Each spider was observed for 15 sec at 0930, 1100, 1400, 1600, 1800, 1930, and 2000 hrs, just before the lights went off. The location of each spider and whether it was spinning was recorded. These records were kept for each spider, starting with its first instar and continuing until it died, escaped, or reached its fifth instar. Sometimes, for inadvertent reasons, some observations were missed on certain days. When spiders were checked between 2000 and 2200 hrs, a flashlight was used. The 11 x 8 x 6 cm plastic cages used in the laboratory have been described elsewhere (Jackson, 1974). The light regime for all other spiders was 12L: 12D (lights on, 0800 hrs).

Except where noted otherwise, data will be given as means \pm S.D. All statistical tests are described in Sokal and Rohlf (1969).

Field Procedures For Investigating Prolonged Use of Nests—Spiders were marked at Mt. Diablo by forcing them from their nests under rocks and taking them into glass shell vials, plugged with cotton. The vials were placed inside a thermos bottle containing crushed ice. As soon as the low temperature had made the spiders sluggish, they were

placed on a sheet of white paper and marked with different colors of enamel paint, applied to the dorsal abdomen with an insect pin. A single spot, less than 1 mm in diameter, was made. The spiders were marked in April, at which time all spiders at Mt. Diablo were either adults or large immatures that would mature at their next molt. When spiders were marked in the laboratory, there was no evidence that this procedure impaired their health or diminished their longevity. The spiders were marked in late afternoon (1500 to 1800 hrs), not all on the same day. After marking, each spider was released beside its nest, which it subsequently re-entered, and the rock was returned to its original position. A metal stake bearing a code number was placed beside the rock to expedite locating it on subsequent visits.

Each marked rock was checked at one to three day intervals, usually two days, each time in the late afternoon. Whenever the marked spider was not found at the marked rock, a search was made of an area within a 4 m or greater radius of the marked rock. The search consisted of overturning each rock greater than 5 cm in length. (*P. johnsoni* have not been found in nests under rocks smaller than this.) If the marked spider was located at a new site, this was marked with a new stake and code number. If the spider was not located, the area was searched at 1 to 3 day intervals for at least 2 weeks subsequently. In some cases, marked spiders were found away from the marked rocks; but at the next check they were again at the marked rock. These were recorded as having been at the same nest site at the previous check as well, since it is strongly suggested that the spider returned to its nest before night.

Laboratory Procedures For Investigating Prolonged Use Of Nests—Two adult females, each in a nest with eggs at the time, were collected from Mt. Diablo in late spring. Two days later, each was placed inside a separate terrarium. Beginning the next day, the location of each spider was systematically recorded until it died. However, it did not prove feasible to follow a strict routine for this. Whenever I was in the laboratory, I checked the spiders at 0930, 1100, 1400, 1600, and 2000 hrs, just before the lights went off. Sometimes some of the check-times were missed, and a number of entire days were missed because I was unable to be in the laboratory. However, the longest period I was away at one time was 12 days. Occasionally spiders were observed continuously for up to several hours at a time.

The terraria, made from clear plastic, were 56 cm long, 53 cm wide, and 30 cm tall. There was a 10 cm diameter rock near the center of the floor of each terrarium. Mineral oil rendered the walls of the terraria too slippery for the spiders to climb. Pupae of house flies (*Musca domestica*) were added every two weeks to a glass dish on the floor of the terrarium. As a result, adult flies were continually present, feeding on sugar kept in three other glass dishes. Each 3 cm diameter dish was approximately 8 cm from a different corner of the cage. Moisture was provided by means of a cotton roll that passed through a hole in the wall of the cage, the exterior end situated in a glass beaker filled with water. The lid of each terrarium was fitted with four evenly spaced ventilation holes (7.5 cm diameter), each covered with metal screen. The floor of each terrarium was covered with sand.

RESULTS AND DISCUSSION

Location Of Nests—Most nests were found associated with wooden boards, fence posts, dead trees (Pt. Reyes, Inglenook), or rocks (all other census areas). Many of those on dead trees were under loose bark. They were found underneath, on sides, and inside

crevices of wood and rocks. In the census areas and other locations, occasionally nests were found underneath dried dung (cow and horse), inside tin cans, and inside dry, hollow reeds (standing or lying on the ground).

Since previous collecting indicated that *P. johnsoni* were not found under rocks or pieces of wood with length less than 5 cm, these were checked only sporadically during censuses. All rocks and wood larger than this were checked during each census. Occupied nests tended to be found under larger rocks and wood, even when those less than 5 cm were not considered (Table 1).

The exact locations of 87 nests (each occupied by *P. johnsoni*) were recorded at Tilden. Most (78%) were on the sides of rocks. The remainder were completely under the rocks. Most (53%) of those on sides of rocks were less than 1 cm above the ground, although some were as high as 8 cm above the ground. In virtually every case, another rock, grass, or other vegetation covered the side of the rock, concealing the nest. The nests under rocks were 1.2 ± 0.83 cm from the side of the rock.

In the laboratory, most nests were constructed in corners; i.e., at locations where three (50%) or two (35%) of the six sides of the cage met ($n=241$). Corners may be optimal for building a nest with an adequate degree of three-dimensionality, and a corner may more closely simulate a concealed location on a rock.



Fig. 1.—Nest of *P. johnsoni*. Shape: T-nest, (see text). D: door. Other two doors obscured by debris (L: leaf; T: twig). Nest fastened to piece of wood (W). Scale: numbers on ruler 1 cm apart.

Shape And Size—Nests consisted of sheets of white silk enclosing a hollow interior, usually with two doors (Fig. 1). A door is an elastic opening through which the spider enters and departs. Four shapes were most common, each named for the letter of the alphabet that it most closely resembled. Ones shaped like straight tubes, normally with a door at each end, are called "I nests." Ones with two arms, each approximately perpendicular to the other, are called "L nests." Nests with arms making an angle closer to 45° are called "V nests." On L and V nests there were normally two doors, one at the end of each arm. Nests with two arms at one end, approximately perpendicular to a third arm, are called "T nests." These usually had three doors, one at the end of each arm. In both the laboratory (64%) and the field (89%), I nests were the most common shape; L nests (laboratory, 22%; field, 3%), V nests (14%, 3%), and T nests (0%; 5%) were less common (laboratory, $n = 241$; field, Tilden, $n = 87$). In the laboratory, spiders frequently occupied the same nest for prolonged periods, and sometimes they slowly changed I nests into L nests or T nests. In the percentages given here, these were recorded as I nests.

At Tilden, 69 I nests occupied by adult *P. johnsoni* were measured to the nearest millimeter. The distance between the two doors is defined as the length. For width, measurements were made across the nests perpendicular to the axis connecting the doors, at the widest location on the nest. Also, the widest diameter of the widest door was measured. Length was 25.3 ± 6.19 mm; width, 16.4 ± 4.89 mm; door width, 11.1 ± 1.48 mm. Since adult spiders tended to be 8 to 10 mm in length (Jackson 1978), nests tended to be approximately two to three times longer than the spider.

Other Characteristics—Nests vary in density (Table 2), but tended to be at the greater end of the density scale. Nests in which spiders molted or oviposited in the field were usually of density value 5 (87%). In the laboratory normally several days (9.4 ± 6.31 , $n = 94$, $\text{min} = 1$, $\text{max} = 28$) passed between initial construction and the time when nests became of density value 5. Occasionally nests of density value 1 were seen in the laboratory, but never in the field.

In the laboratory, older nests tended to take on a torn or shredded appearance ("ragged"), and these nests were usually abandoned by the spiders in the laboratory. Raggedness of nests was judged on a scale from 1 (not at all ragged) to 6 (ragged to such a degree that it was barely recognizable as a nest). During Census No. 2 at Tilden (Table 1), the raggedness of 112 nests (25 occupied by *P. johnsoni*, 87 not occupied) was recorded. The occupied nests were less ragged (raggedness-value 1, 40%; 2, 40%; 3, 12%; 4, 4%; 5, 4%; 6, 0%) than ones that were not occupied (1, 4%; 2, 22%; 3, 23%; 4, 21%; 5, 15%; 6, 15%) (Mann Whitney U-test, $p < 0.001$).

Nests in ragged condition in nature were frequently impregnated with debris, such as small stones and vegetable matter (Fig. 1). Clutter was judged on a scale from 1 to 5 (1, no debris; 2, ca. 25% of nest surface covered by debris; 3, ca. 50% covered; 4, ca. 75% covered; 5, ca. 100% covered). Considering the same 112 nests from Tilden Census No. 2, occupied nests were less cluttered (1, 44%; 2, 44%; 3, 8%; 4, 44%; 5, 0%) than unoccupied ones (1, 10%; 2, 45%; 3, 30%; 4, 10%; 5, 5%) (Mann Whitney U-test, $p < 0.001$).

Sometimes spiders eventually constructed a second chamber on older nests, usually with the doors of the two chambers superimposed. When a male cohabits with a subadult female (Jackson 1976), he constructs a second chamber on the female's nest, with the doors of his chamber superimposed on those of the subadult's. Occasionally when the nest of the subadult already had two chambers, the male cohabited in the existing second chamber, rather than constructing a new chamber himself.

Table 1.—Size of rocks (Tilden, Mt. Diablo, Whiskey Mountain, Pothole Dome) and pieces of wood (Pt. Reyes, Ingleenook). Ones with compared to ones without nests occupied by *P. johnsoni* (t-tests; t-values given when significant, * $P < 0.05$, ** $P < 0.001$). All rocks or wood in census area with occupied nests measured. For those not occupied, a sector of the census area was selected randomly. Length: the greatest distance across rock or wood in a plane parallel to ground. Width: distance across in same plane as length but perpendicular to the length. Height: greatest distance across in plane perpendicular to ground. Only rocks and wood with length 5 cm or greater measured.

Census	Area of sector (sq. m)	Rocks or wood with occupied nests	Number	Length (cm)	Width (cm)	Height (cm)
Tilden No. 1	290	Yes	62	42.9 ± 16.71	27.4 ± 10.77	21.3 ± 10.87
		No	143	40.4 ± 21.39	26.7 ± 13.13	20.6 ± 16.61
		t		n.s.	n.s.	n.s.
Tilden No. 2	232	Yes	25	40.6 ± 21.56	33.5 ± 31.80	19.3 ± 12.62
		No	87	30.2 ± 20.54	20.8 ± 14.39	8.6 ± 6.12
		t		n.s.	2.350*	5.816**
Mt. Diablo No. 1	279	Yes	36	20.1 ± 7.34	15.7 ± 5.87	13.2 ± 5.79
		No	108	11.2 ± 5.23	7.9 ± 4.17	4.3 ± 2.72
		t		7.937**	8.817**	12.425**
Mt. Diablo No. 2	186	Yes	31	16.5 ± 5.51	11.7 ± 4.11	8.4 ± 2.46
		No	64	11.4 ± 5.71	8.1 ± 3.58	4.6 ± 3.96
		t		4.108**	4.320**	4.905**
Pt. Reyes No. 1	93	Yes	11	69.6 ± 59.46	10.2 ± 3.76	4.1 ± 1.70
		No	140	42.16 ± 47.19	7.6 ± 4.04	3.3 ± 2.06
		t		n.s.	2.017**	n.s.
Pt. Reyes No. 2	84	Yes	16	87.9 ± 95.55	15.2 ± 11.28	8.1 ± 8.15
		No	192	26.4 ± 23.01	7.6 ± 4.52	3.0 ± 2.64
		t		6.949**	5.514**	5.805**
Ingleenook	1510	Yes	20	129.0 ± 64.16	8.6 ± 2.90	3.3 ± 1.45
		No	105	74.7 ± 61.82	11.2 ± 16.97	4.1 ± 10.95
		t		3.583**	n.s.	n.s.
Whiskey Mountain	41	Yes	5	20.8 ± 8.69	12.7 ± 1.80	4.6 ± 2.13
		No	170	20.1 ± 13.56	14.0 ± 9.55	6.6 ± 5.28
		t		n.s.	n.s.	n.s.
Pothole Dome	51	Yes	9	21.8 ± 11.91	16.0 ± 8.03	6.9 ± 3.10
		No	189	18.5 ± 14.91	13.2 ± 10.82	5.1 ± 3.68
		t		n.s.	n.s.	n.s.

Table 2.—Silk density of nests from census areas: 1, very little silk, only minimally structured as a nest (doors not distinct); 2, nearly transparent, but distinctly structured as a nest; 3, translucent; 4, nearly opaque; 5, completely opaque. Data expressed as the percentages of nests of a given category (percentage of N) having the specified densities. Each nest occupied by a living *P. johnsoni*: F, adult female only; M, adult male only; F, M, or I, either an adult female, adult male, an immature spider (exclusive of postembryos and first instars), or an adult male with an adult or immature female. Progeny: mass of postembryos or first instar spiderlings.

OCCUPANTS OF NESTS			SILK DENSITY OF NEST					N
Sex/Age Class	Exuvium	Progeny	1	2	3	4	5	
M, F, or I	No	No	0%	2%	19%	26%	53%	1280
M, F, or I	Yes	Yes or No	0%	0%	1%	17%	82%	136
F	No	Yes	0%	0%	0%	4%	96%	135
F	No	No	0%	3%	24%	20%	53%	205
M	No	No	0%	13%	56%	15%	16%	62

Patterns Of Occupation—Various observations suggest that it is adaptively very important for *P. johnsoni* to occupy nests at night. When censuses were made in the field at sunrise, all the *P. johnsoni* located were occupying nests (Jackson 1978). In the laboratory, when spiders ($n = 322$) were placed in clean cages, most (89%) built nests within 24 hrs, either before the lights went off or during the dark period in the laboratory.

Spiders with nests were only very rarely found outside their nests during the dark period in the laboratory; and in each case, the spider was inside its nest by morning. Nest departure occurs soon after the lights come on in the morning. However, observations in the field suggest that this is an artifact related to the constant warm temperature in the laboratory. In the field, spiders evidently depart nests later in the morning, after the ambient temperature has risen (data not collected). During the afternoon, the spiders gradually enter their nests in the laboratory (Table 3). Thirty minutes before the lights went off in the laboratory, fewer than 10% of the spiders were generally outside their nests, and most of these usually entered their nests by the time the lights went off, suggestive of a circadian rhythm.

In the laboratory, the total amount of time that spiders remained in their nests was rather large, and this may be partly an artifact related to the continual supply of food (2 to 8 living flies maintained in each cage at all times). A major internal factor influencing the spider's tendency to depart may be hunger, and in the laboratory spiders may remain satiated most of the time. This could be easily tested by maintaining spiders on differing feeding schedules.

Spinning Inside Nests—Spiders apparently spend much time spinning while occupying their nests. The data in Table 3 probably underestimate the percentage of the spider's time occupied with spinning each day, since each spider was observed only briefly and spinning was not recorded unless it happened to occur at the time of observation. Spinning was seen especially in the late afternoon and early morning. However, relatively little spinning occurred at the time just before the lights went off and in the dark. The majority of spinning that was seen took place in old nests; i.e., ones that had been present from a previous day. However, of those spiders spinning at the time the lights went off and in the dark, relatively many were spinning in new nests. Possibly the number of spiders spinning in the dark was particularly subject to underestimation by the methods employed here, since turning the flashlight suddenly on the spiders may have caused startle responses in which they ceased to spin.

Nest Occupation And Molting—Very likely, spiders are especially vulnerable to predation at the time of molting. At least during the molting process itself, the spider is unable to actively defend itself, and possibly it has reduced mobility, sensory acuity, and

Table 3.—Nest related behavior of spiders reared in the laboratory. N: total number of observations made at the indicated times. Inside nest: percentage of the total number of observations during which spiders were located inside nests. Spinning: percentage of the observations of spiders inside nests during which the spiders were spinning. Spinning in Old Nest: percentage of observations of spiders spinning during which the nest was an old nest (present from a previous day). Lights on: 0900; lights out: 2000 hr. See text for details.

Time (hr)	0930	1100	1400	1600	1800	1930	2000	Dark
INSIDE NEST	72	68	72	81	92	92	97	100
SPINNING	6	2	1	2	5	6	2	1
SPINNING IN OLD NEST	95	100	89	96	92	94	83	60
N	1583	1804	2044	1623	1722	617	1580	380

other functions. In the laboratory, spiders remained in their nests for a number of days preceding (5.9 ± 3.35 days, $n = 95$) and following (2.3 ± 1.67 days, $n = 156$) molting. The postmolt period may be related to inactivity by the spider as its cuticle hardens, and the premolt period may be a period of inactivity by the spider as it makes physiological preparations for molting. Comparing (t-tests) the premolt period for the molt on which spiders became mature (prematurity molt) to all previous molts and comparing the premolt period at the prematurity molt for males and females, there were no evident differences. This was also true for postmolt periods.

Nomadic Males And Sedentary Females—Previously (Jackson 1978) the hypothesis was put forth that males of *P. johnsoni* are adapted to a life style that emphasizes searching for females and mating at the expense of maintenance and survival. Consistent with this, males in the field were found in nests of lesser density than those of females (Table 2, Mann Whitney, $P < 0.001$). Also, disproportionately many males were located outside nests compared to females and immatures (Table 4).

Location Of Spiders When Not Occupying Nests—A total of 150 individuals were located outside nests in the field. Half (75) were not near a nest; 7 were on a rock or piece of wood with a nest underneath or on the side; 16 were under a rock or piece of wood with a nest present; 8 were standing on a nest; and 44 were standing beside (within 1 cm) of a nest. From these data and from observing spiders in the field and the laboratory, it seems that when spiders depart their nests they often remain quite near the nest, although at other times they go considerable distances from the nest. Further information was provided by observations on marked spiders.

Marked Spiders In The Field—At Mt. Diablo marked spiders frequently remained at the same nest site for a number of days (minimum estimate, 7.1 ± 10.40 days; maximum estimate, 10.1 ± 10.89 days; $n = 16$). When spiders were not found, predation may have occurred or they may have moved outside the area searched. In three cases spiders were found at nests other than the ones at which they were marked. 1. An adult female that was not found on the day after marking was located in a second nest under a different rock, 0.6 m away, 3 days later. 2. Another adult female that was not found on the day after marking was found 14 days later in a second nest under a rock 4 m away. 3. An adult male was initially found inside a nest with an exuvium (large palps on exuvium), presumably having recently molted. He was not found the next day, but 4 days later he was located in a second nest, touching the old nest, under the same rock. Twelve days later, this male was not present; but an adult female was inside the nest. She was marked, re-located at the same nest on the next check-day (2 days later), then not seen again.

Three marked spiders were observed to depart and return to the same nest. 1. An adult female was found 3 cm from her nest, but under the same rock, on the fifth day after marking. Later in the day, she was found inside her nest again. Incidentally, this spider

Table 4.—Comparison of frequencies with which spiders of each sex/age class were found inside versus outside nests. Summed data from all censuses in which at least one male, one female, and one immature were found. Data for males compared to summed data for females and immatures indicate that males were found more often outside nests ($G = 37.634$, $P < 0.005$).

	PERCENTAGE INSIDE NESTS	PERCENTAGE OUTSIDE NESTS	NUMBER
ADULT MALES	68.93	31.07	103
ADULT FEMALES	92.25	7.75	284
IMMATURES	92.58	7.42	283
ALL SEX/AGE CLASSES	88.81	11.19	670

remained at the same nest for one month (maximum estimate, 33 days; minimum, 28 days), the greatest period in this study. 2. Another adult female was located on three different days outside her nest. Each time, she was found inside her nest again at the next check. Five days after marking, she was under a rock 30 cm away from the one with her nest. There was no nest under this rock. Once on the second day and again on the eighth day after marking, she was found 1 cm from her nest but under the same rock. 3. A subadult female was found under a rock 1.2 m from her nest on the fifth day after marking. There was no nest under this rock. At the next check, 2 days later, she was inside her nest again. This spider remained at the same nest for 3 weeks (maximum, 24 days; minimum, 22 days). On the 24th day after marking, an exuvium with paint marks was inside the nest, but the spider had departed. Another subadult female also remained at the same nest for 3 weeks (maximum, 23 days; minimum, 21 days). On the 21st day after marking, an exuvium with paint plus an adult female was found in the nest. Two days later, the female had vanished. Another subadult female remained at one nest only briefly (maximum, 3 days; minimum, 1 day). Three adult males and one adult female were not found again after marking. Another five adult females were found at the same nest for only 1 to 6 days.

In the laboratory and the field (Mt. Diablo and Tilden), males were found to cohabit with subadult females for as long as 2 weeks (Jackson, 1976a). The two subadult females in this study that remained at single nest sites for 3 weeks each before molting, with no males present, demonstrate that prolonged residence by subadult females at single nests is not unique to situations involving cohabitation.

Spiders In Terraria—Each female constructed two nests, each in a corner of her terrarium (i.e., where two walls and the floor came together). The rock was not used as a nest site by either spider, and it was generally observed in the laboratory that when spiders were provided rocks inside terraria and plastic cages, they nevertheless built their nests on the walls of the container rather than on the rocks.

Each spider built its first nest by the first evening, later abandoned this nest, and did not subsequently use it. In the discussion that follows, all references to the spiders' nests refer to the second nests. One spider built its second nest four days after being placed in the terrarium; and the other spider, after five days. One spider oviposited two batches of fertile eggs, followed by an infertile batch. The other spider oviposited three batches of fertile eggs. Each batch was oviposited at approximately one month intervals in the same nest. In effect, each spider had a nest containing either eggs, spiderlings, or both during the entire summer and early fall. Assuming that the same nests were used on days when observations were not made, each spider used a single nest for 6 to 7 months.

Although the two females spent a great deal of their time inside their nests (Table 5), they sometimes departed the nest, usually remaining in the close vicinity of the nest; but sometimes they were seen as far away as the opposite side of the terrarium. Each time, after departing, the female returned to her nest by evening. This behavior persisted after oviposition ceased; and in each case, after the female died, her corpse was found outside but near her nest. The data for the females are consistent and they are pooled in Table 5.

As mentioned earlier, the continual supply of prey in the laboratory may have resulted in the spiders remaining inside their nests a disproportionately greater time than would have been the case in nature.

Field Observations Concerning Multiple Batches In Single Nests—In the field, more than one batch was found in a single nest on seven occasions, each time with an adult female inside the nest. Nests containing both eggs and a set of spiderlings were found five

times. On three occasions, two sets of egg shells were found inside single nests. Most likely, these were cases in which females remained at the same nest at least long enough to produce two batches.

Use Of Nests Built By Other Individuals—On four occasions, two exuvia of different sizes were found inside the same nest. Possibly, the same spider remained at the nest long enough to molt twice. However, individuals of *P. johnsoni* will occupy nests that they do not construct, as has been noted for other salticid species as well (Crane 1949, Gerhardt 1921, Plett 1962). In the laboratory, when a spider was removed from its cage and a different spider was placed inside the cage, the new spider frequently employed the previous spider's nest. They occupied these overnight, sometimes longer, and occasionally molted or oviposited inside them. There was evidence that this occurred in the field also. Once a large exuvium was found in a nest containing eggs. There was no spider present. One possibility is that a subadult molted and matured in this nest, mated, and finally oviposited in the same nest. Another possibility is that an immature used this nest as a molting site after a previous female had oviposited here, or vice versa. On three occasions, relatively large exuvia were found inside nests with egg shells. In one case, the exuvium came from a male, as indicated by the enlarged palps. Twice exuvia were found that were considerably larger than the spider that occupied the same nest at the time, indicating that these nests had been previously occupied by different spiders.

Plett (1962) found that large individuals of the salticid *Salticus scenicus* will take over the nests of other individuals. This has not been seen in the field for *P. johnsoni*, although aggressive interactions leading to this result have been witnessed in the laboratory (Jackson 1976a).

GENERAL DISCUSSION

Homing Behavior—When Plett (1962) marked *Salticus scenicus* Clerck in the field with colored dots, he found no evidence of homing behavior or a tendency to repeatedly use the same nest. In contrast, *P. johnsoni* seems to make prolonged use of single nests. They depart and return to the same nest site after excursions of as far as 1.2 m. It would be valuable to investigate potential homing mechanisms, including kinesthetic mechanisms and visual orientation by means of landmarks, sun position, and the plane of polarization of sunlight. Chemical trail following, perhaps associated with draglines, might be con-

Table 5.—Pooled data for two adult females kept in individual terraria. The number of days on which observations were made at each time was one-half the number of observations, because 2 observations (2 spiders) were made at each check-time. Considering only those observations during which spiders were outside nests, the percentages at different locations are provided in the last 4 rows: A, on nest; B, within 2 cm of nest; C, more than 2 cm from nest but on same side of terrarium; D, on other side of terrarium. Lights on: 0900, lights out 2000 hr. See text for details.

Time (hr)	0930	1100	1400	1600	1800	2000
No. of Observations	356	332	340	320	308	352
Inside Nest	97%	92%	93%	94%	97%	100%
Outside Nest	3%	8%	7%	6%	3%	0%
A	60%	38%	50%	44%	60%	---
B	20%	15%	8%	33%	20%	---
C	20%	32%	17%	11%	20%	---
D	0%	15%	25%	11%	0%	---

sidered, although this seems a less likely possibility. Orientation by sun position and by plane of sunlight polarization have been demonstrated in agelenid (see Schoer 1974) and lycosid (see Magni *et al.* 1965) spiders, and Land (1969) discussed morphological features that might be related to discrimination of the plane of polarization in the eyes of *P. johnsoni* and other salticids.

Function Of Nests—Adaptive radiation in a group of animals can be viewed as the product of an evolutionary lineage entering a new adaptive zone (Simpson 1953). In the case of spiders, the adaptive zone is probably somehow related to the use of silk. Some of the web building spiders are extremely dependent on silk, with almost every event in their lives involving silk in some intimate manner. Although the salticids are not so extreme, the construction and use of silk nests is integral to understanding the adaptations of *P. johnsoni* and no doubt other salticids.

The daily routine and life history of the spider is very much centered around the nests, which are occupied each night, and in which molting, mating and oviposition take place. Courtship behavior is adapted to nests. Nests, in the laboratory and nature, are used repeatedly over a period of days, with the spider departing and returning to the same nest. Although the time and energy investments put into nests have not been measured, they may be considerable. Much time seems to be spent spinning and most spiders in the field were found occupying relatively dense nests. Nests occupied by spiders in the laboratory acquired comparable density only after several days of occupancy. These factors may favor individuals that make more or less prolonged use of their nests.

One major function of nests is probably protection from predators during periods, such as at night and during molting, when the spider is inactive and probably especially vulnerable. Females remain with their eggs inside nests, and perhaps protect the eggs from predators and parasites. Mating often occurs inside nests, and the spiders are probably safer from predation inside compared to outside nests during courtship and copulation (Jackson 1976b).

Nests might function in keeping the occupants dry. Often after a heavy rain, drops of water were seen on the exterior of nests in the field, and the surroundings of the nests were sometimes very wet. However, the occupants of nests rarely showed signs of having become wet. At most there might be a few drops of water on their bodies and legs. Another possibility that has not been explored is that the interiors of nests remain at more constant temperature and humidity than the surroundings.

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NEST ASSOCIATES OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE)

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ABSTRACT

Spiders (Gnaphosidae, Clubionidae, etc.), insects (Collembola, Lepidoptera, etc.), and other invertebrates (mites, isopods, millipedes, and snails) were found inside, on, under, and beside nests of *P. johnsoni*. Some nest associates were found at nests that were occupied by *P. johnsoni* at the time, but most were at unoccupied nests. Dead organisms, in some cases possibly prey remains of *P. johnsoni*, and exuvia of other organisms were found also. Hypotheses concerning the adaptive significance of associations are discussed, including predation on *P. johnsoni* and their eggs, scavenging, and the use of *P. johnsoni* nests as shelters.

INTRODUCTION

Adaptive radiation in spiders has led to a great diversity of adaptations related to the use of silk. In many cases, structures such as webs, egg cases, and nests are constructed by the spider and remain in the environment for some time afterwards. These may be involved in functions related to prey capture, protection from predators, communication, and other aspects of the spider's biology. However, use of these structures is not restricted to the individual or the species that constructed them, since other organisms may form various types of associations with the silken constructions of spiders. This paper will consider organisms that associate with the nests of the salticid spider *Phidippus johnsoni* Peckham and Peckham.

Vagabond spiders such as the salticids do not build prey capturing devices from silk. However, many build nests (retreats) in which they may molt, mate, oviposit, and remain when inactive. Although associates of the web-building spiders have attracted considerable interest, associates of the nests of vagabond spiders have received relatively little attention.

Some species of spiders are apparently specialized as predators of web-building spiders in their webs, and these are frequently found in the webs of their prey (Bristowe 1958, Czajka 1963). Other species are "kleptoparasites" (Bristowe 1958, Legendre 1960, Vollrath 1976). Sometimes the webs of one species of spider have lines fastened to webs

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of another species. Also, one may find one species inside an occupied web of another species, as an occasional rather than a routine occurrence, and predation on insects in the host's web or on the host itself may occur (Bentzien 1973, Bristowe 1958, Crocker and Felton 1972, McCook 1889, Roberts 1969). Various insects are sometimes found in the webs of spiders, in which they may feed on prey caught in the web or prey remains left by the host; or they may be predators or parasites of the spider or her eggs (Bristowe 1941, China and Myers 1929). Various salticid species will enter both occupied and unoccupied webs of other spiders, sometimes building their nests there, and sometimes preying on the host (Bristowe 1941, Jackson 1976, McCook 1889, Nielsen 1931, Robinson and Valerio 1977, Tolbert 1975). Various insects and foreign spider species live in the webs of "social" spiders (Brach 1977, Diguët 1915, New 1974), and generally the adaptive significance of these associations are poorly understood.

The data in this paper were collected in conjunction with studies of the reproductive biology and life history of this species (Jackson 1976a, 1978a, b). During the course of these studies it was possible to become quite familiar with the shape, size, and texture of *P. johnsoni* nests and to distinguish them from those of other common sympatric vagabond spiders that use the same nest sites, primarily gnaphosids and clubionids. It became apparent that other species are frequently inside nests built by *P. johnsoni*, and data were collected concerning these. Since this species occurs at rather high densities in the field (2 to 30 per 1000 sq. m.; Jackson 1978a), both occupied and unoccupied nests of *P. johnsoni* would seem to be potentially important physical features in these habitats, making the associates of this species of special interest.

METHODS AND MATERIALS

The species involved in this study was determined as *P. johnsoni* from descriptions provided by Peckham and Peckham (1900, 1909) and from labeled museum specimens, including ones identified by the Peckhams. The spiders that Peckham and Peckham (1909) identified as *P. formosus* are apparently the same species as *P. johnsoni* (Jackson, unpublished data). Kaston (1972) noted this also. Spiders of the *formosus* form are found especially in southern California. In this study, spiders from Santa Barbara and Palomar were primarily ones of the *formosus* form. In the remaining populations, the *johnsoni* form predominated.

Whenever an organism other than *P. johnsoni* was found inside, underneath (between the nest and the rock, piece of wood, etc.), on (touching the nest but not underneath), or beside (within a few millimeters of the nest) the nest, it was collected, if possible, and notes were made concerning the nest and its contents. The primary habitats from which these data came were the census areas (Jackson, 1978a), similar neighboring areas, plus several additional habitats not previously described. Each study site will be briefly characterized here, with information given in the following order: location, elevation (recorded as nearest 500 m), plant community, description, primary nest sites (in parentheses). The classification system of Munz (1959) is used for California plant communities.

- A. Tilden—Coastal Range (California, Contra Costa Co.). 500m. Coastal Prairie. Rocky, grass covered slopes (rocks).
- B. Mt. Diablo—Coastal Range (California, Contra Costa Co.). 1000m. Foothill Woodland. Rocky, grass covered slopes (rocks).

- C. Santa Barbara—Coastal Range (California, Santa Barbara Co.). Santa Ynez Mountains. 500m. Valley Grassland. Rocky, grass covered slopes (rocks).
- D. Palomar Mountain—Transverse Ranges (California, San Diego Co.). 1500m. Southern Oak Woodland. Rocky, grass covered slopes (rocks.)
- E. Point Reyes—Beach (California, Marin Co.). Sea level. Coastal Strand. Sand dunes near ocean (wood on ground).
- F. Inglenook—Beach (California, Mendocino Co.). Sea level. Coastal Prairie and Coastal Strand. Sand dunes and bluff near ocean (wood on ground, fence posts, dead trees).
- G. Pothole Dome—Alpine (California, Mariposa Co.). Sierra Nevada. 2500m. Lodgepole Forest. Open, rocky areas on granite dome (rocks).
- H. Tenaya Lake—Alpine (California, Mariposa Co.). Sierra Nevada. 2500m. Lodgepole Forest. Open, rocky areas on granite dome (rocks).
- I. Whiskey Mountain—Alpine (Wyoming, Fremont Co.). Rocky Mountains. 3000m. Timberline. Extremely rocky slopes (rocks).
- J. Blacktail Butte—Subalpine (Wyoming, Teton Co.). Rocky Mountains. 2000m. Conifer forest. Open, rocky areas within forest (rocks).

RESULTS AND DISCUSSION

Many spiders (77) were found associated with nests of *P. johnsoni* (Table 1). Of these, 61 percent were gnaphosids. Sixty spiders, including 42 gnaphosids, were inside *P. johnsoni* nests; insects (17) and other invertebrates (7) were found less frequently. These seem to be less prone to be inside the nests, since only nine insects and two other invertebrates were found inside nests. In addition, dead organisms and exuvia were sometimes found associated with *P. johnsoni* nests. Except for springtails, mites, and ants, only one living individual nest associate was found at any given nest, although a *P. johnsoni* might be present at the same nest with the associate.

An estimate for the proportion of the total number of nests occupied by nest associates was obtained from monthly censuses at Tilden, Mt. Diablo, Pt. Reyes, and Inglenook (Jackson, 1978a), pooling data for all months and all habitats. Also, for this subset of the data, only those organisms actually inside nests were considered. Of the 4,137 *P. johnsoni* nests encountered, 69% were occupied by *P. johnsoni* at the time. Nest associates were not found in any of the nests containing *P. johnsoni* during the censuses, but they were found inside 4.1 percent of the remaining nests, or 1.3 percent of the total number of nests encountered. The potential nest-associated predator of *P. johnsoni*, *Herpyllus hesperolus* Chamberlin (Jackson 1976b), was found inside two of the *P. johnsoni* nests in these censuses.

Any nests for which there was doubt concerning the species by which it was built were not counted. Consequently, estimates are conservative. There are no apparent differences in the empty versus occupied nest ratios in the different habitats or for different habitats or for different times of the year.

Springtails And Mites—Two very common types of nest associates are not listed in Table 1, springtails and mites (Anystidae). These small arthropods were frequently seen in, on, under, or beside nests, especially ones not occupied by *P. johnsoni*, but also ones that were still occupied. Often they were associated with nests containing other nest associate species, exuvia, eggshells, or other contents. The mites and springtails sometimes occurred at the same nests together. Sometimes the bright red anystid mites were present

Table 1.—Living organisms found associated with nests of *Phidippus johnsoni*. Except when otherwise stated, the associate is mature. For associates not identified to species, the lowest taxonomic determination is given. Numbers refer to the total number of nests occupied by the indicated associate; parenthetical breakdown refers to numbers found inside the nest, under the nest, on the nest, and beside the nest, respectively. Letters refer to habitats in which a given associate was found (see Methods and Materials).

ASSOCIATES	NUMBER	HABITATS
Araneae		
Gnaphosidae		
<i>Zelotes</i> sp.	34 (31, 1, 1, 1)	A, B, E, F, G
<i>Herpyllus hesperolus</i> Chamberlin	7 (5, 0, 0, 2)	A, B
<i>Drassodes neglectus</i> Keyserling	2 (2, 0, 0, 0)	I
<i>Gnaphosa muscorum</i> C. L. Koch	1 (1, 0, 0, 0)	I
<i>Gnaphosa brumalis</i> Thorell	1 (1, 0, 0, 0)	I
<i>Haplodrassus</i> sp.	1 (1, 0, 0, 0)	D
Undetermined genus	1 (1, 0, 0, 0)	C
Clubionidae		
<i>Clubiona californica</i> Fox	7 (7, 0, 0, 0)	E, F
<i>Clubiona</i> sp. 1	5 (5, 0, 0, 0)	A, B
<i>Clubiona</i> sp. 2	1 (1, 0, 0, 0)	H
<i>Scotinella</i> sp.	2 (1, 1, 0, 0)	A
Agelenidae		
<i>Calilena restricta</i> Chamberlin and Ivie	5 (0, 0, 0, 5)	B
Dictynidae		
<i>Dictyna</i> sp.	2 (1, 1, 0, 0)	F
Erigoniidae		
Undetermined genus	2 (1, 1, 0, 0)	B, F
Salticidae		
<i>Talavera minuta</i> Banks	2 (1, 1, 0, 0)	A
Thomisidae		
sp. 1	2 (1, 0, 1, 0)	F
sp. 2	1 (0, 0, 1, 0)	A
Amaurobiidae		
<i>Titanoeca sylvicola</i> Chamberlin and Ivie	1 (0, 1, 0, 0)	I
Lycosidae		
<i>Pardosa</i> sp.	1 (1, 0, 0, 0)	F
Insecta		
Lepidoptera		
Unidentified larvae	4 (4, 0, 0, 0)	A, B
Unidentified pupa	1 (0, 0, 1, 0)	A
Dermaptera	4 (3, 1, 0, 0)	A, F
Hymenoptera		
Formicidae	3 (1, 0, 2, 0)	F, J
Coleoptera		
Elateridae	2 (0, 2, 0, 0)	F, I
Staphylinidae	1 (1, 0, 0, 0)	B
Thysanura		
Lepismatidae	1 (0, 1, 0, 0)	F
Crustacea		
Isopoda		
<i>Armadillidium vulgare</i> Latreille	4 (2, 1, 1, 0)	E, F
Diplopoda	1 (0, 1, 0, 0)	F
Gastropoda	2 (0, 0, 2, 0)	F

in numbers in excess of 30 at nests not occupied by *P. johnsoni*. When, as often occurred, smaller numbers of mites or springtails were present, they were not so conspicuous and careful searching was necessary in order to discover them. In general, records were not kept of these arthropods.

Vagabond Spiders—Of the spiders listed in Table 1, salticids, gnaphosids, clubionids, thomisids, and lycosids are vagabond species. For molting and oviposition, and in some species during periods of inactivity in general, these spiders go inside nests that they construct from silk. These are usually tubular structures, not so unlike those of *P. johnsoni* in their general form. Many of the observations of individuals from these groups occupying *P. johnsoni* nests may have been cases of the spider simply making use of an available nest that it did not itself construct. The adaptive significance of this could be related to avoiding the expenditure of time and energy that would have been necessary in order to construct a nest of its own. Also, a nest of *P. johnsoni* might be preferable in some ways to nests the associate could construct. For example, the nests of *P. johnsoni* tend to be rather large and densely woven with silk (Jackson 1978b). In comparison, the nests built in the laboratory by *H. hesperolus*, *Zelotes*, and the unidentified *Clubiona* from Tilden are not very densely woven, and the nests these spiders were found occupying in the field when not inside *P. johnsoni* nests were relatively flimsy in appearance. The larger, more dense nests of *P. johnsoni* might provide greater protection from predators, parasites, dessication, or other perils for these spiders than the nests they construct themselves.

The salticid *Talavera minuta* Banks warrants special mention. Adults of this species are much smaller in body size than *P. johnsoni*. The one found under a *P. johnsoni* nest was inside a nest of its own, which differed in appearance and was much smaller than *P. johnsoni* nests. A few other individuals of this species were found at Tilden in similar nests, under rocks. In the case of the *T. minuta* found inside a *P. johnsoni* nest, this nest was considerably larger than the spider.

In the case of the *Drassodes neglectus* Keyserling and one of the unidentified *Clubiona* from Tilden, an exuvium was in the nest with the spider. These exuvia presumably came from the nest associates, since size and eye arrangement were appropriate for the associates in each case. On two occasions at Mt. Diablo, a large gnaphosid exuvium, probably of *H. hesperolus*, was found in a nest not containing spiders. Twice, an exuvium of a gnaphosid (one, probably of a *Zelotes*; the other, probably of a *Herpyllus*) was found in a *P. johnsoni* nest with a *P. johnsoni* exuvium. The following gnaphosids were found inside *P. johnsoni* nests with *P. johnsoni* exuvia: *Zelotes*, 4; *Herpyllus hesperolus*, 1; *Haplodrassus* 1; and *Gnaphosa muscorum* C. L. Koch, 1. Clearly, spiders occupy nests that they do not themselves construct. Whether or not spiders that occupy the nests of other spiders spin inside them or otherwise alter them is not known.

One of the *Zelotes* was found inside a *P. johnsoni* nest with dried *P. johnsoni* eggs, and possibly these were eaten by the gnaphosid. There was a living immature *P. johnsoni* inside the nest on which the *Scotinella* sp. was found.

Gnaphosids As Predators—Except for *Zelotes*, the gnaphosids in Table 1 were of size comparable to or larger than the adults of *P. johnsoni*. The two individuals of *Drassodes neglectus* were found inside nests containing dead *P. johnsoni*, which had probably been killed and eaten by the gnaphosids. In the case of one of the two *H. hesperolus* found beside a nest, there was an immature *P. johnsoni* inside. The other *H. hesperolus* was inside a nest resembling those that this species constructs itself, fastened at one end to an empty *P. johnsoni* nest. In the case of one of the *H. hesperolus* inside a nest, an immature

P. johnsoni was standing beside the nest. Laboratory experiments indicated that *H. hesperolus* will prey upon *P. johnsoni* that they find in nests. Males of *P. johnsoni* have alternative forms of courtship (Jackson 1977a), one of which is vibratory in nature and performed on the nests of females. In the laboratory, *H. hesperolus* sometimes prey upon males that court at nests constructed by *P. johnsoni* females but occupied by the gnaphosids (Jackson 1976b). Similar predation might occur on females and immatures of *P. johnsoni*, when they depart then return to the same nest or enter nests built by other conspecifics (Jackson 1978b). Further study is needed in order to ascertain the importance of this type of predation as a selection factor favoring gnaphosids associating with *P. johnsoni* nest.

Web-Building Spiders—Amaurobiids and dictynids are web-building spiders, but there were no webs in the vicinity of the individuals found associated with *P. johnsoni* nests. Probably they were simply taking temporary shelter at the nests.

Each agelenid found beside a *P. johnsoni* nest was in a web that was attached to and partially covered the *P. johnsoni* nest. In each case, a live *P. johnsoni* was inside the nest. More information is needed before much can be concluded concerning the relationship between the agelenids and the salticids in these instances. Perhaps the web touches the nest purely by chance, as a result of being built under the same rock. Although salticids are known to place their nests near or in webs of other spiders (McCook 1889), this seems less likely in these cases because the agelenid webs partially covered the salticids nests, rather than vice versa, suggesting that the webs were built after the nests. Perhaps the silk nests are particularly sturdy or easily employed attachment sites for webs compared to the rock or vegetation.

Other Invertebrates—The nests of *P. johnsoni* may be convenient, suitable shelters for various organisms besides spiders, perhaps largely accounting for many of the insects and other invertebrates found inside and under nests (Table 1).

Concerning the lepidopteran larvae inside *P. johnsoni* nests and the pupa on a nest, perhaps the nests of *P. johnsoni* provide an especially suitable site for some lepidopterans to construct their cocoons when they pupate. Possibly these lepidopterans augment the silk that they produce with the existing silk of the nest.

Each of the two nests at which ants were found at Blacktail Butte contained dead *P. johnsoni* (one, a male; the other, a female plus eggs). Approximately five of these small black ants were found at each nest. They were on the outside only of the nest containing a dead female; but both outside and inside the nest containing the male. It would seem probable that ants feed on dead *P. johnsoni* and possibly their eggs when they find them. Considering the small size of the ants, the possibility that they kill *P. johnsoni* before feeding seems less likely. At Inglenook a single small black ant was found on a nest occupied by a female *P. johnsoni*. Possibly various organisms are prone to enter *P. johnsoni* nests and feed on dead *P. johnsoni* or their eggs, but more information is needed concerning this. In the laboratory, *P. johnsoni* that spontaneously died were sometimes inside their nests when found (Jackson 1978a).

An exuvium of an earwig was found on an empty nest, and another was found inside a nest occupied by an immature *P. johnsoni* plus a *P. johnsoni* exuvium.

Dead Organisms—Dead organisms were sometimes found on the surface of *P. johnsoni* nests. A small gastropod shell at Tilden and a dead millipede at Inglenook were probably fortuitous events. Other cases may have been remains of prey left by *P. johnsoni* at their nests. *P. johnsoni* have been seen in the field and the laboratory standing beside their nests while feeding. Three *Pardosa* (Lycosidae), seven large flies, one honeybee worker

(*Apis mellifera*, Apidae), one aphid (Aphidae), and one stink bug (Pentatomidae) had the appearance of prey fed upon by *P. johnsoni* (i.e., they were dry, hollow, macerated carcasses). With the exception of the stink bug, *P. johnsoni* have been observed in nature feeding on members of each of these groups (Jackson 1977b). In some cases, *P. johnsoni* were inside the nests on which the dead organisms were found: one of the *Pardosa*, five of the flies, the honeybee, and the stink bug.

Parasitoids and Parasites—One acrocerid fly larva emerged from an immature *P. johnsoni* in its nest and pupated in the laboratory (collected at Del Puerto Canyon near Mt. Hamilton, California). The spider probably would have died in its nest if it had been in nature. The acrocerids are parasitoids on spiders (Bristowe 1941, Schlinger 1960).

Egg parasites have been reared from nests of several *Phidippus* species (Coquillett 1892, Davidson 1896, Edwards 1975), although they have not been reported so far for *P. johnsoni*.

***Phidippus Johnsoni* Inside Gnaphosid Nest**—More than 3500 *P. johnsoni* have been observed in nature inside nests. Only once was one found inside a nest clearly of another species. This was an adult male at Mt. Diablo found inside a relatively large nest that resembled closely those constructed by *H. hesperolus*. Perhaps it is significant that this was a male, since males seem to have a life style that emphasizes searching for females and mating (Jackson 1978a, b). Females and immatures may be more sedentary. A nomadic male might be the most likely class of *P. johnsoni* to take refuge in a nest it did not itself construct, even rarely those of other species.

GENERAL DISCUSSION

Although generally this is not a phenomenon that has attracted much attention, there are sufficient reports in the literature to suggest that association between organisms of various types and the nests of vagabond spiders are fairly common. Yates (1968) and McCook (1889) reported several cases of one species being found on or inside the nests of another species. Myers (1927) noted that ladybird beetles (*Rhyobius ventralis*) sometimes occupy deserted nests of the salticid *Holoplatys senilis* Dalmat. Also they may be found inside nests occupied by the salticid simultaneously, but inside a different chamber. Lamoral (1968) studied four species of intertidal, non-salticid spiders that build nests in mollusk shells, crevices of rocks, and similar locations. One species frequently occupied nests of the other species rather than building ones of its own. Also these spiders often feed at the nest, and a springtail was found at the nests as a scavenger. China and Myers (1929) reported instances of hemipterans found in nests of oxyopid spiders.

Auten (1925) discussed organisms found associated with nests containing eggs of the vagabond spider *Philodromus canadensis* Emerton (Thomisidae) plus those of some web spiders, two Araneidae and one Theridiidae. She concluded that there were three types of associates: parasites, predators, and accidental inhabitants. The present report for the salticid *P. johnsoni* differs in a number of ways. Auten restricted her study to nests containing eggs, while our study included all nests regardless of the presence or absence of eggs or spiders. This may have accounted for some differences, such as the failure in our study to find the parasites and parasitoids of eggs and spiders Auten found (Ichneumonidae, etc.). The major group of nest associates found in this study was other spiders, a group not reported in Auten's study. The predators that she found were probably primarily predators of eggs and young spiderlings, while possible predators of adults and larger immatures were found in our study.

Considering Auten's study in conjunction with ours, classes of possible nest associates of vagabond spiders can be summarized as follows:

1. Parasites and parasitoids of spiders that seek out and/or emerge from their hosts inside nests.
2. Parasites of eggs in nests.
3. Predators of eggs and spiders in nests.
4. Scavengers feeding on dead spiders in nests.
5. Predators that adopt nests as a predatory device. This might include the gnaphosids that prey on *P. johnsoni* males that court at nests built by *P. johnsoni* females, but occupied by the gnaphosid. (Jackson 1976b).
6. Nest-building spiders that adopt nests of other species as a substitute for constructing their own nests.
7. Organisms that adopt nests as a particularly suitable refuge or pupation site. More work is needed to determine how sharp the distinction is between this category and the next one.
8. Accidental inhabitants, or ones that just happen to be in or around the nest, and for which the association has no particular significance.

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ASPECTS OF THE COURTSHIP BEHAVIOR OF THE BLACK WIDOW SPIDER, *LATRODECTUS HESPERUS* (ARANEAE: THERIDIIDAE), WITH EVIDENCE FOR THE EXISTENCE OF A CONTACT SEX PHEROMONE

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ABSTRACT

The courtship and mating behavior of the black widow spider, *Latrodectus hesperus* Chamberlin and Ivie, were studied to determine stimuli responsible for mate location and courtship initiation in this species. We observed new courtship patterns which included a vigorous display performed by females, "push-ups" executed by both sexes, and cryptic abdominal vibrations produced by males immediately upon contact with female webs. Males initiated courtship when they contacted unoccupied conspecific female webs, but did not respond when placed on other male webs. Male *L. hesperus* also initiated courtship behavior on unoccupied female webs of another species, *Latrodectus mactans* (Fabricius). Female *L. hesperus* were stimulated by contact with conspecific male webs, but not other female webs. Scanning electron microscopy revealed what are presumed to be chemoreceptive hairs on the tarsi and pedipalps of males and females. We conclude that male and female *L. hesperus* produce sexually specific, complementary contact pheromones which are incorporated into their silk. These substances apparently function in mate location, sex identification, and courtship for this species, but not as an isolating mechanism between *L. hesperus* and *L. mactans*.

INTRODUCTION

Courtship and mating behavioral patterns of black widow spiders, *Latrodectus* spp., have been described by Herms et al. (1935) and D'Amour et al. (1936). Kaston (1970) added important details to these descriptions; however, questions concerning mate location and the stimuli responsible for causing males to initiate courtship remain unanswered.

Montgomery (1910) and Hewitt (1917) first suggested that contact-chemical and tactile cues may be important in sexual and species recognition by nocturnal web-building arachnids. Subsequently, Gerhardt (1924), Locket (1926) and Bristowe (1929) observed that male web-spinners were sexually stimulated upon contact with the female's web. Experiments on vagabond spiders led Kaston (1936) to conclude that both contact chemoreception and visual clues were used in mate location by members of this group. Hegdekar and Dondale (1969) demonstrated the existence of a contact sex pheromone in the threads of lycosid spiders. Their study revealed that the pheromone is species-specific,

stable in air, and secreted only by adult females, regardless of their prior mating experience. Blanke (1973) examined the sexual behavior of the tropical Araneid *Cyrtophora cicatrosa* and found that males were attracted to empty bags previously occupied by females, indicating an olfactory sexual pheromone. No data are available on the cues used by males of any species of *Latrodectus* to locate females, or on the stimuli responsible for releasing courtship behavior.

Several workers have searched for chemoreceptors in spiders. Kaston (1935) presented evidence suggesting that the slit or lyriform organs were chemosensory, but electrophysiological experiments later showed these structures to have a mechanoreceptive function (Walcott and Van der Kloot 1959). Blumenthal (1935) indicated his belief that the "tarsal organs" were chemoreceptors; however, these structures occur on the proximal ends of tarsi and palps and would, therefore, not normally contact chemically active substrates. Foelix (1970) identified curved, blunt-tipped hairs on the legs of spiders which he presumed to be chemoreceptors. These hairs featured an open tip to a lumen and were distributed on all tarsal segments. That they closely resemble chemosensitive hairs on the antennae of insects and were found in all spiders studied, seems quite persuasive. No species of black widow spider was among those Foelix examined.

This study was initiated to determine the role of contact chemoreception in the reproductive behavior of *Latrodectus hesperus* Chamberlin and Ivie. We report previously underscribed male and female courtship patterns which were used in experiments to behaviorally bioassay the chemical activity of webs. We also present scanning electron micrographs of *L. hesperus* tarsi which reveal what are presumed to be contact chemoreceptors.

GENERAL METHODS

Latrodectus hesperus of both sexes and all developmental stages were collected in the fall of 1977 in Phoenix and Tucson, Arizona. Four specimens of *Latrodectus mactans* (Fabricius) were acquired from east central Oklahoma, near Okemah. Individuals were isolated in 30 x 70 mm amber plastic vials in the laboratory and fed mealworms (*Tenebrio* sp.) and pink bollworm larvae (*Pectinophora gossypiella*). Courtship was staged in 11 x 12 cm plastic containers and the chemical activity was behaviorally bioassayed on those webs constructed in plastic vials. More than 25 courtship encounters were staged and observed. Unless otherwise indicated, all experiments were conducted on a sample size of seven. Individuals used in experiments were tested once in 24 hours. Male and female tarsi and pedipalps were mounted on aluminum pegs with double sticky cellophane tape, vacuum coated with gold-palladium, and observed on an Etec Autoscan scanning electron microscope. Scanning electron micrographs were produced with Type 55 pos-neg Polaroid film.

RESULTS

Courtship.—The courtship and mating behavior of *L. hesperus* generally conformed to the descriptions of previous workers. A synthesis of previous accounts and our observations follows: Males charged their palpal organs with semen shortly after the definitive molt. Thus equipped for mating, they generally showed heightened levels of activity over earlier instars. They abandoned their webs and no longer actively captured prey. (One male was observed to feed on the captured prey of a female in her web). Upon entering a

female's web, the typical male began his courtship display which consisted of tapping and tweaking the lines with his front tarsi. While so doing, the male explored the web cautiously, rhythmically tapping the silk with his pedipalps. During this period of exploration, the male's body jerked spasmodically and the abdomen was vibrated at a high frequency. Periods of rest interspersed active searching and display. The female frequently initially rejected the display and charged the male, in which case the male beat a hasty retreat or silked from the female's web.

Approaching the female cautiously, the male usually cut the web at strategic points, effectively reducing the female's potential routes of escape. At this point, the courting male caressed the female's legs, then her abdomen, and ultimately climbed excitedly over her body (Figs. 1a and b). A courting male was frequently observed to "throw silk" about the female, forming the so-called "bridal veil." He then positioned himself venter to venter with his mate. Successful males then located the female epigynum and inserted first one, then the other, palpal organ. The time consumed in courtship was highly variable, with a range of from 10 minutes to 2 hours. Males that succeeded in insemination lingered in the vicinity of their mates or wandered leisurely away. This was in marked contrast with the initial cautious approach and escape strategies characteristic of males prior to insemination. Only one male of those we observed to succeed in inseminating a female was eaten by his mate immediately after mating. However, several were later found dead in their mates' webs.

Gerhardt (1924) and others (see Kaston 1970) have indicated that the male loses the distal end of the embolus during copulation. This loss may subsequently render the male impotent. If this is the case, successful males would best serve their biological interests by presenting themselves to their mates as a post-nuptial meal. In so doing, a male would contribute to the production of eggs that he would posthumously fertilize. If the female is sufficiently well-fed to decline this offer immediately after copulation, the male should have no better purpose than to linger on the web until such time as the female's appetite returned.

New Courtship Patterns.—We observed several previously undescribed behavioral patterns in the courtship of *L. hesperus*. Not previously noted was occasional extreme aggressivity of females in courtship. Eager females exhibited jerky movements and repeated violent twitches of the abdomen. These patterns were identical to male courtship behavior but they appeared to be more violent, owing to the much larger size of the female. Males responded positively to female displays and these events usually resulted in successful insemination of the female.

Both sexes were consistently observed to execute "push-ups" (i.e., alternate flexion and extension of the legs) while courting, but this pattern also routinely occurred in the context of disturbance. While viewing males through a dissection microscope, we noted that the male abdomen usually began vibrating shortly after the individual had made contact with the female's web. These vibrations had escaped our preliminary unaided observation. We also noted that shortly after the onset of abdominal vibration, and before they had contacted the female, males began to "throw silk" with their hind legs. Furthermore, males trailed silk while searching the female web. Subsequent experiments revealed that abdominal vibration and silk throwing occurred on webs unoccupied by female spiders, suggesting that males were responding to contact with the web in the absence of visual clues. We, therefore, suspected the presence of a contact pheromone in the web of the female and designed experiments to test this hypothesis.

Contact Pheromone Experiments.—Abdominal vibrations and body tremors of adult male and female *L. hesperus* were used in behavioral bioassay experiments to determine the presence of a contact pheromone in the web of this species. The occurrence of these patterns was scored as a positive response. If these patterns did not occur, a negative response was noted.

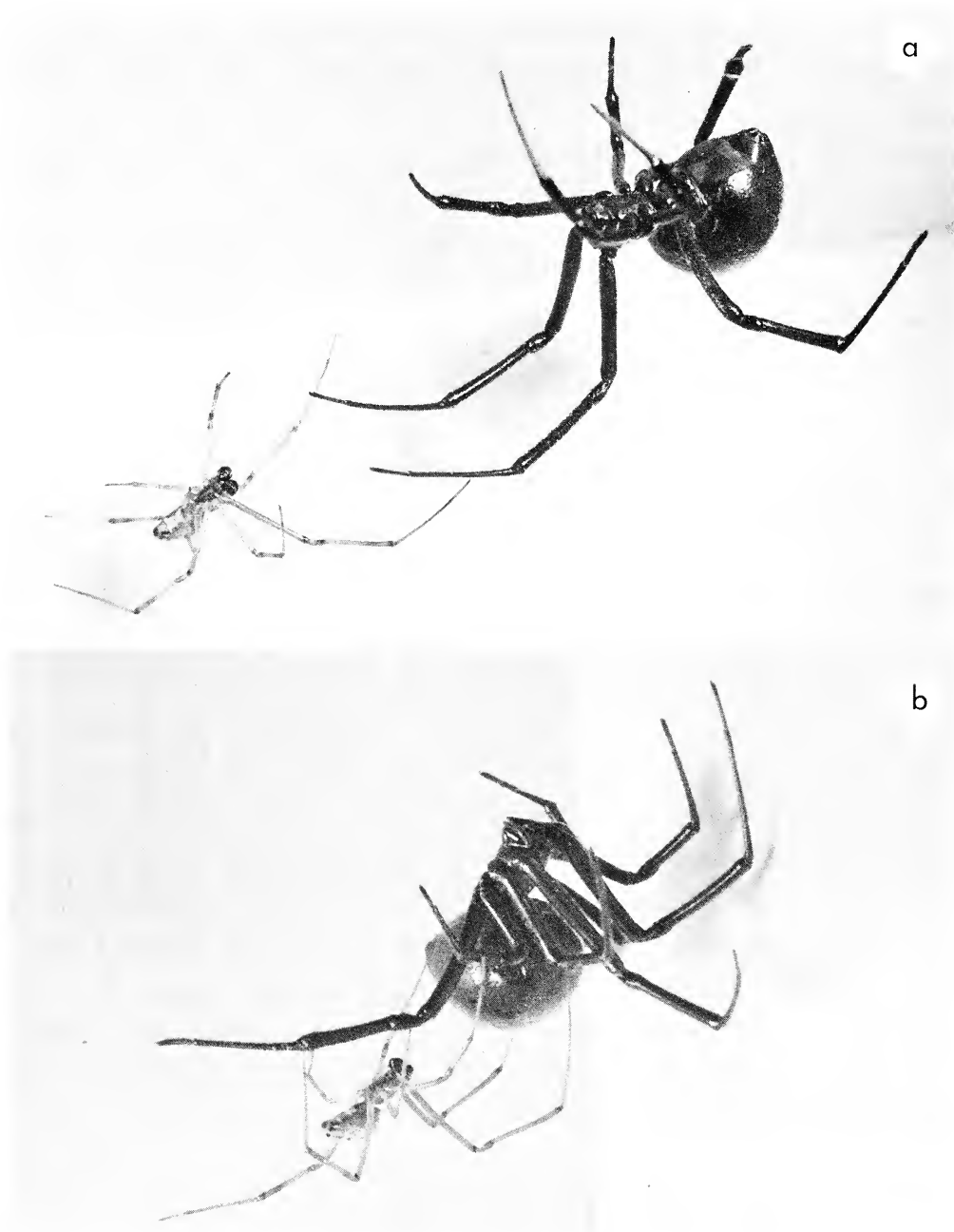


Fig. 1.—Contact between a courting pair of black widow spiders: 1a, leg to leg contact (direct tactile stimuli are exchanged in this essential step); 1b, leg to body contact (during this step the male may wrap the female with his threads).

Male spiders ($n=7$) were placed on male webs from which the original occupants had been removed. Each was observed for 10 minutes. In no case did the tested males show indications of sexual excitement, but the introduced males actively explored the webs on which they had been placed. Adult males ($n=7$) were placed on unoccupied female webs and observed as before. All males responded positively (i.e. with abdominal vibrations) shortly after contact with the female web.

We next attempted to determine if males were responding to the physical structure or chemical content of the female webs. Adult female webbing was removed from containers and compressed into small balls to disrupt its physical properties. These were then placed into vials into which candidate males were introduced. All males tested exhibited signs of sexual excitement when they contacted compressed balls of a female web. This result seemed to support the contact pheromone hypothesis.

We attempted to determine how long the female webs would retain their ability to stimulate males. Unattended webs were left exposed to open air and males were tested daily on these. The results of this experiment were variable (Table 1). Three males continued to be sexually stimulated on webs that had been exposed to air for over 2 weeks. In one case, a male responded to a vacant female web for 50 days, at which time he died. Four of the unoccupied female webs elicited a male response for no longer than three days.

We next tested the activity of webs produced by immature females. Males were placed on unoccupied webs of fourth and fifth instar females and observed as before. In all but one trial, the males reacted positively, although their behavior patterns seemed to be qualitatively less vigorous than those exhibited on adult female webs.

An alternative to the contact pheromone hypothesis was that males were responding to an airborne chemical emanating from the female or her web. To test this possibility, a female was placed in a clean vial for 5 minutes, at which time she and any webbing she had produced were removed. A male was then introduced immediately into the vial. In no case did the male ($n=7$) respond positively. A refinement of this experiment involved placing a partition of perforated aluminum foil over the female and her web in the vial. Males were then placed on top of the perforated foil and observed. None of the males ($n=7$) tested exhibited sexual excitation.

Sexual pheromones have been shown to function in species isolation for a large number of insect species (Jacobson and Beroza 1963). We wondered if the chemical present in the web of *L. hesperus* was species-specific. To check this possibility, we placed an *L. mactans* adult male on seven different webs of female *L. hesperus*. Before each trial, an *L. hesperus* male was used to validate the activity of the conspecific webs. All webs elicited a positive response from *L. hesperus* and surprisingly also from the *L. mactans* male. A modified reciprocal of this experiment was conducted. Male *L. hesperus* ($n=7$) were placed on the webs of *L. mactans*. No *L. mactans* males were available to test the activity of conspecific female webs, so *L. hesperus* were tested first on the nonspecific web, then for the sake of comparison, on the webs of *L. hesperus* females. *L. hesperus* males reacted positively to all webs, but showed a qualitatively more vigorous response to conspecific webs.

Finally, we wished to determine the response of females to conspecific male webs. All females ($n=7$) exhibited the excited movements previously observed in response to male courtship. This behavior was again strikingly similar to the courtship behavior of the males. As a control, females were placed on the unoccupied webs of other females. In three trials, the females showed no reaction whatsoever. Four of the seven responded by

Table 1.—Duration of sexual responsiveness of males to webs of females exposed in open air.

Specimens tested	Duration of sexual response
Male 212 on web of female 17	3 days
Male 210 on web of female 1	2 days
Male 206 on web of female 19	14 days
Male 206 on web of female 10	2 days
Male 206 on web of female 7	2 days
Male 224 on web of female 406	50 days (male died)
Male 202 on web of female 413	16 days

exploring the new web for a short period of time. The exploratory behavior lacked the components which were elicited in response to contact with male webs.

Chemoreceptors.—Scanning electron micrographs of the tarsi and pedipalps of *L. hesperus* revealed what are presumed to be the chemosensory hairs described by Foelix (1970) for other web-building spiders (Figs. 2b and c). These are arranged in parallel rows pointed toward the distal end of the appendages and inserted at an angle of about 80° to the axis of the leg. They are blunt (open) tipped, slightly curved structures, etched in a spiral pattern. The hairs measure 50-60 μm in length, and have a diameter of ca. 5 μm at the base and 2 μm at the tips. Each is inserted in a crater-like socket. These structures are uniformly distributed on all tarsal segments, (Fig. 2a) and on the ventral surface of the palpal organs in both sexes. These are the anatomical parts which contact the web during courtship.

The presumed chemoreceptors are distinct from mechanoreceptors, in that the latter are at least five times longer than the former. Also, the mechanoreceptive hairs form an angle of less than 30° with the axis of the appendage, and they are inserted on conical processes. They are sharp-pointed rather than blunt, and have no end opening.

DISCUSSION

Our data strongly suggest that *L. hesperus* males locate conspecific females and identify potential mates by contact with the female web. Furthermore, it is apparently a chemical component or components of the web and not its physical structure to which males are responding. This system surely functions to the advantage of both sexes. The female spider's web effectively extends her appendages several hundred times in length, and the volume of space she commands by an equivalent factor. If in the evolution of these spiders, some females produced chemicals (perhaps metabolic wastes) and excreted these into their silk, and some males in the population possessed receptors tuned to these chemical cues, both the producers and recipients of this information would have enhanced probability of meeting and mating. This mutual advantage has apparently resulted in selection favoring co-evolutionary refinement of the system.

Vagabond spiders of the families Salticidae, Pisauridae, and Thomisidae, phylogenetically subordinate to the Theridiidae, do not construct webs and rely on direct contact to exchange chemical stimuli important in species and sexual recognition (Kaston 1936). Wolf spiders (Lycosidae), a somewhat more highly evolved family, illustrate a

possible transitional condition. They rely on direct contact, and females produce small temporary threads which contain contact sexual pheromones (Kaston 1936, Hegdekar and Dondale 1969). The system of web-borne contact chemical communication may reach its highest development in the Araneidae, the orb weavers, a group characterized by the production of very large and elaborate webs.

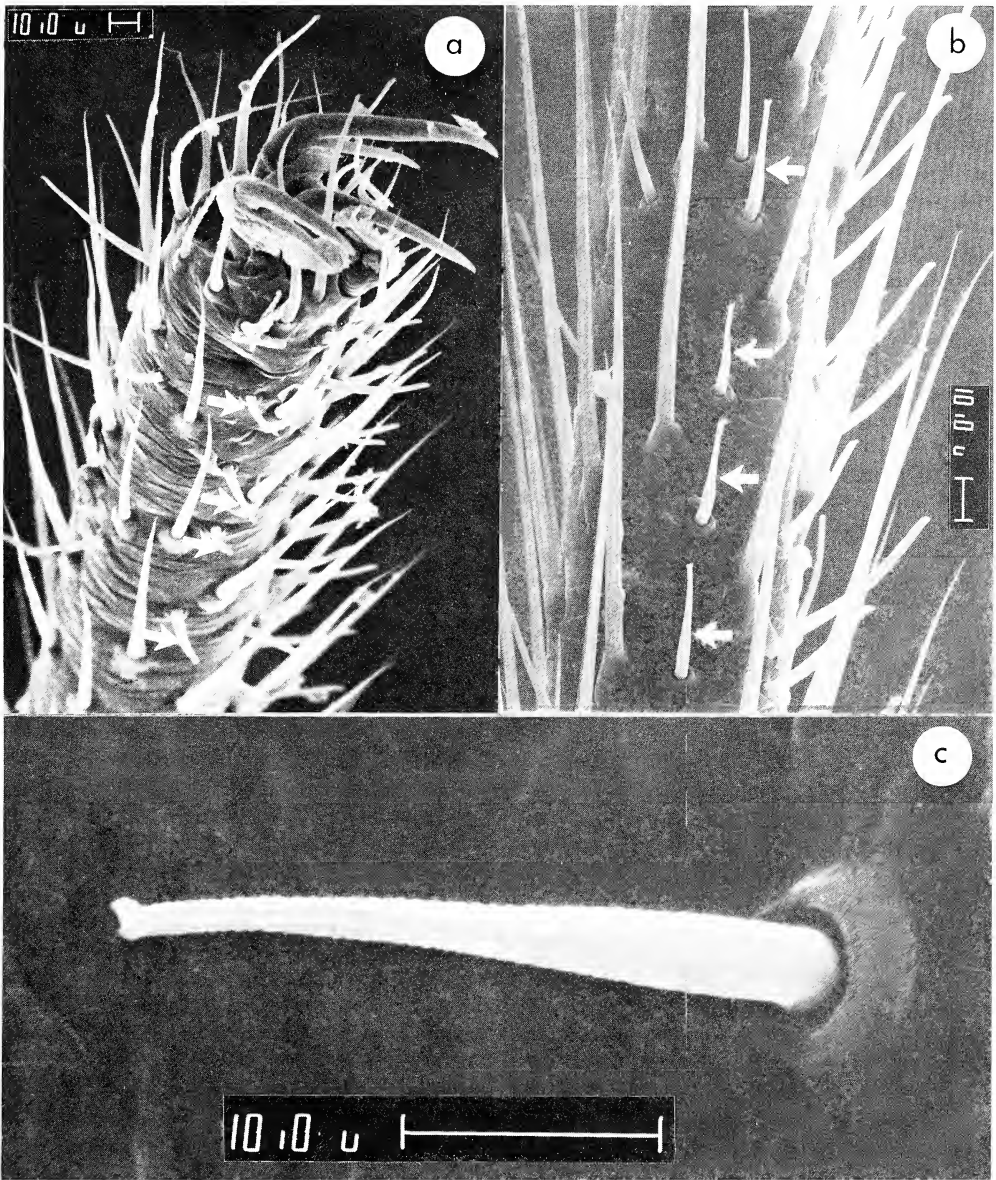


Fig. 2.—Scanning electron micrographs of structures on adult male black widow spiders: 2a, apical tarsal segment showing row of presumptive contact chemosensitive hairs (indicated by arrows) towards the apex of the tarsus; 2b, curved, blunt-tipped presumptive chemosensitive hairs (arrows) occur in longitudinal rows, with rows of pointed mechanoreceptive hairs between them; 2c; close-up of an individual presumptive chemosensitive hair, note spiral texture, open tip, and crater-like insertion.

We were somewhat perplexed that the contact pheromone in the web of *L. hesperus* is apparently not distinct from that produced by the closely related species, *L. mactans*. The precise distribution of the two species is not known, however, Kaston's (1970) distributional notes suggest that the two species are allopatric; hence, there has been no selection favoring divergence in the chemical components between the two. Also, it is unlikely that the pheromone produced by the two species would chemically differentiate by genetic drift if they consist of essentially unmodified metabolites. Significantly, Kaston (1970) was able to stage three successful matings between *L. mactans* and *L. hesperus* in the laboratory, indicating that premating isolating mechanisms between the two are not highly developed. We assume that the active substances in female webs are sufficiently different from those of other less closely related species in the family and members of other families so that male black widows are able to avoid dangerous and wasteful courting on heterospecific webs.

Another problem arises from our discovery that the webs of sexually immature and mated adult females as well as those of adult virgins are chemically active. This condition might work to the detriment of males because it would cause them to waste time courting unreceptive females. Chemically active webs could, on the other hand, be of considerable benefit to their immature or previously mated adult female occupants in that courting males are potential prey. The initial cautious behavior of males on conspecific female webs would seem to reveal their innate awareness of this danger. Indeed, Bristowe (1929) speculates that the marked sexual dimorphism manifest in web spinners is an adaptation that enhances male agility and escape potential on female webs.

Kaston (personal communication) has suggested another explanation for the apparent chemical activity of immature female webs. A male that contacts an immature female web may (cautiously) linger on it until the female has undergone the definitive molt, at which time the patient male would be rewarded with a receptive potential mate. This system would be mutually advantageous to both sexes. It might be particularly advantageous to the male if there is high risk involved in searching for female webs. This hypothesis is clearly in need of further study. (Subsequent to Dr. Kaston's communication, we have observed four instances of adult male *L. hesperus* waiting on immature conspecific female webs in the field. Although we did not see mating, in each case males remained unmolested on immature female webs for several days).

Abdominal vibrations by both sexes seem to be important initial components in courtship. The male apparently immediately announces his presence on the female web using this behavioral pattern and his mechanical message is communicated via the web to the female. Females almost certainly use this information to distinguish courting males from captured prey. The female, if she is receptive, responds to the male vibrations in kind, thus encouraging the male.

Female responsiveness to male webs revealed by our experiments seemed anomalous in that females probably do not search for males, and adult males do not construct webs. Reproductive males do, however, produce silk while courting. It may be that in close encounters between the sexes, females chemically validate the identity of the male by contacting the silk he throws to produce the "bridal veil." It was apparent to us that the "bridal veil" symbolically, rather than physically, binds the female. The female could easily break the binding threads, but may be inhibited from doing so by her perception of their chemical content, a possible complementary male pheromone.

To summarize, it appears likely that black widow spiders incorporate complementary contact sexual pheromones into their silk and that these are detected by chemoreceptors

in the legs and palps of the opposite sex. The female-produced pheromone serves to aid the male in gross location of a conspecific mate and releases his initial courtship behavioral patterns. The male-produced pheromone inhibits the female's predatory response and probably lowers her threshold for mating readiness.

ACKNOWLEDGMENTS

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A NEW SPECIES OF *APOCHTHONIUS* CHAMBERLIN FROM OREGON (PSEUDOSCORPIONIDA, CHTHONIIDAE)

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ABSTRACT

A subterranean pseudoscorpion species, *Apochthonius forbesi*, new species, is described from a lavatube sink in central Oregon; it is compared, both morphologically and ecologically, to *A. malheuri* Benedict and Malcolm from Malheur Cave, southeastern Oregon.

INTRODUCTION

Although my recent biogeographical study of Oregon pseudoscorpions has revealed that specimens of the genus *Apochthonius* Chamberlin are the most commonly collected leaf litter inhabiting forms in western Oregon (Benedict 1978), only a very few records of the genus have been reported previously for the state. Chamberlin (1929) described *A. occidentalis* Chamberlin from one male collected from moss at Portland (Multnomah County). Benedict and Malcolm (1973) described *A. malheuri* Benedict and Malcolm from nine specimens recovered from well-rotted wood chips in Malheur Cave (Harney County), and reported *A. minimus* Schuster from one specimen taken in litter of western red cedar (*Thuja plicata* Donn), from east of Steamboat (Douglas County). Muchmore and Benedict (1976:68) in a redescription of the type species of the genus, *Apochthonius moestus* (Banks), also mentioned a "moestus-like" female from litter of mountain spray (*Holodiscus dumosus* (Hook.) Heller), on Steens Mountain (Harney County). The present paper provides a description of a new species which inhabits the mossy-litter layer beneath mountain spray growing in the bottom of the sink in which Charcoal Cave No. 1 of the Arnold Lavatube System (Deschutes County) is located (Greeley 1971).

Apochthonius forbesi, new species

Type record.—Oregon: Deschutes Co., 14 km S, 11 km E of Bend (1385 m), mosses and leaf litter of mountain spray, 20 May 1972 (E. M. Benedict), 1 male (holotype AMNH), 1 female (allotype AMNH).

Etymology.—The specific name is a patronym in honor of Dr. Richard B. Forbes, Professor of Biology, Portland State University, who has greatly encouraged my research of Oregon pseudoscorpions.

Distribution.—Reported only from a single locality in central Oregon.

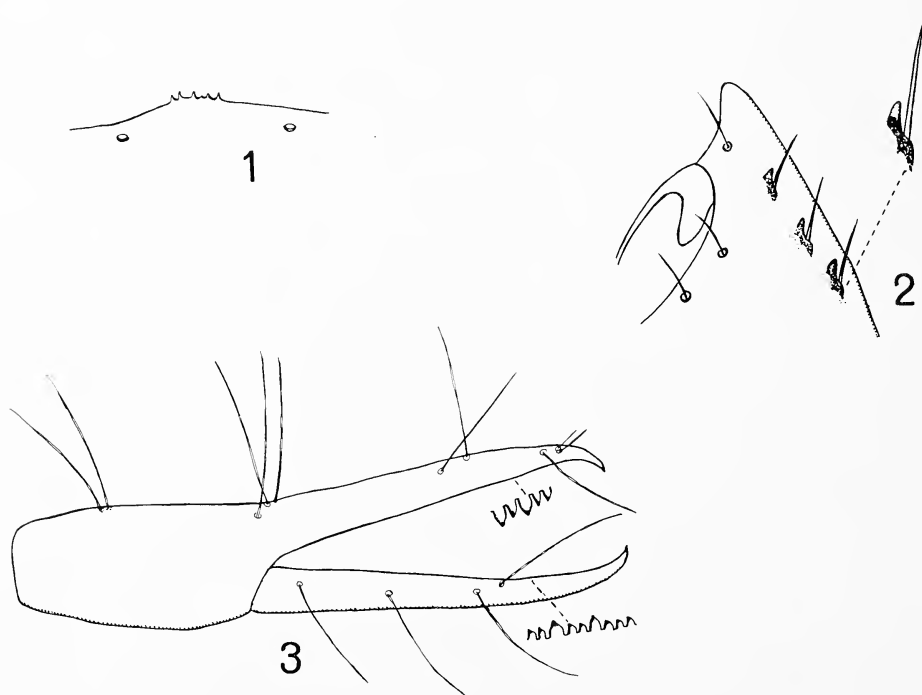
Diagnosis.—With the general features of the genus (see Muchmore and Benedict 1976). A moderately sized species with four very weakly developed eyes and with moderately attenuate appendages; generally similar to *A. malheuri* Benedict and Malcolm (1973), but smaller, slightly stouter and with slightly better eye development.

Description.—Measurements and morphometric ratios in Tables 1 and 2. All sclerotized parts light tan. Derm mostly reticulate throughout.

MALE. Cephalothorax: carapace longer than broad, markedly narrowed posteriorly; anterior margin with small denticulate epistome (Fig. 1) and a few fine denticles laterally; two pairs indistinct eyes, anterior pair located two ocular diameters from anterior carapacial margin, surface of carapace smooth dorsally, becoming somewhat reticulate laterally and posteriorly; chaetotaxy 10-4-4-2-2-4=26, setae shorter than width of palpal femur. Coxal chaetotaxy 2-2-1:0-2-1-CS:2-2:2 or 1-3:2-3; coxa I with elongate, non-setose apical process, and three acute, seta-like coxal spines each with a well-developed, elongate anterior process (Fig. 2); no intercoxal tubercle.

Abdomen: chaetotaxy of holotypic terga 4:4:7:6:9:9:9:9:9:7:6:0; of holotypic sterna 11:(4-4):(2)6-6/5-5(2):(4)8(4):12:12:13:12:14:9:0:mm.

Chelicera: approximately 0.9 as long as carapace; hand with seven setae; fixed finger with approximately 15 marginal teeth, and movable finger with about 12; spinneret a



Figs. 1-3.—*Apochthonius forbesi*, new species, from central Oregon: 1, epistomal area; 2, coxal spine series from coxa I; 3, external aspect of chela.

Table 1.—Measurements and morphometric ratios of *Apochthonius forbesi*, new species from central Oregon. (Abbreviations: B=breadth, D=depth, L=length, ?=indeterminable).

	Measurements (in mm)		Ratios	
	Male	Female	Male	Female
Body L	1.42	1.60		
Abdominal B	?	0.57		
Carapace L	0.46	0.50		
Ocular B	0.39	0.45		
Posterior B	0.33±	0.37		
Chelicera L	0.42±	0.41		
Pedipalp				
Femur L/B	0.55/0.11	0.60/0.12	4.8	4.9
Tibia L/B	0.26/0.14	0.30/0.16	1.9	1.9
Chela L/D	0.85/0.16	0.79/0.17	5.4	4.9
Movable finger L	0.59	0.55		
Hand L	0.27	0.31		
Leg I				
Basifemur L/D	0.30/ ?	0.31/0.07	?	4.6
Telofemur L/D	0.15/ ?	0.18/0.07	?	2.6
Tibia L/D	0.18/ ?	0.21/0.05	?	4.1
Miotarsus L/D	0.38/ ?	0.34/0.04	?	7.8
Leg IV				
Entire femur L/D	0.48/0.18	0.46/ ?	2.7	?
Tibia L/D	0.34/0.08	?	4.4	?
Metatarsus L/D	0.16/0.06	?	2.8	?
Telotarsus L/D	0.30/0.04	0.33/ ?	7.6	?

weakly-developed sclerotic knob; serrula exterior with 20 blades; serrula interior with approximately 12 blades; flagellum of eight long pinnate setae and one short (1/6 length of others) simple seta.

Palp: relatively large and slender. Chelal chaetotaxy and dentition as illustrated (Fig. 3); both fingers with occasional longer, wider teeth interspersed between majority of teeth; fixed finger with approximately 76 teeth, tall quadrangular distally, gradually becoming triangular medially, and basally, merging into acute serrations; movable finger with approximately 68 teeth, distally tall quadrangular, gradually more rounded and lower near finger base. Movable finger with rounded sensillum on external surface, half-way between ST and SB.

Legs: slender. Tactile setae on tibia and both tarsi of leg IV.
FEMALE. Essentially similar to male but more robust. Chaetotaxy of allotypic terga 4:4:8:9:10:10:9:9:9:7:7:0; of sterna 8:(2?)8(3):(3)7(3):12:14:13:15:12:10:0:mm. Fixed finger of chela with 72 teeth, movable finger with 63 teeth.

Nymphal stages are unknown.
Remarks.—In contrast to the other Oregon leaf litter-inhabiting species, *A. forbesi* exhibits somewhat less pigment and/or a thinner cuticle (or both), weaker eyes, slightly slimmer appendages and greater size (Tables 1, 2). “In most epigean forms. . . the femur/carapace ratio is less than 1.1 and the chela/carapace ratio is less than 1.7, while in most of the troglobitic forms the corresponding ratios are greater than 1.15 and 1.75 respectively” (Muchmore 1976:78). The femur/carapace ratio of the holotype (male) of *A. forbesi* is 1.19, while the chela/carapace ratio is 1.86, both suggesting some degree of

Table 2.—Comparison of selected morphometric ratios of the palps and carapace of males of species of *Apochthonius* Chamberlin according to ecological types. (Abbreviations: L=length, W=depth or breadth).

	Epigean spp.	Cave spp.	<i>A. forbesi</i>	<i>A. malheuri</i>
Femur L/W	4.7 mean	5.2 mean	4.8	5.6 mean
Chela L/W	5.0 mean	5.8 mean	5.4	5.7 mean
Femur L/carapace L	<1.1	>1.15	1.19	1.32
Chela L/carapace L	<1.7	>1.75	1.86	1.92

attenuation of the palp. Even though the total specialization of *A. forbesi* for subterranean existence is not as marked as that observed for many cavernicolous species such as *A. malheuri* (Table 2), it is still apparent. For further discussions of the troglobitic tendencies exhibited by species of *Apochthonius*, see Chamberlin and Malcolm (1960), Benedict and Malcolm (1973) and Muchmore (1976).

Ecology.—It is especially noteworthy that *A. malheuri* and *A. forbesi* exhibit some degree of morphological specializations, as both appear to represent separate relict populations occurring in mesic habitats of otherwise semi-arid areas east of the Cascade Mountains of Oregon. Malheur Cave, characterized recently by Palmer (1975) and Benedict et al. (1977) as a moderately warm thermal cave, is located in a grassland-sagebrush (*Artemisia tridentata* Nutt.) area at an elevation of 1220 m where the average annual precipitation is 290 mm. Charcoal Sink, approximately 220 km W of Malheur Cave, is in an area ecotonal between open stands of ponderosa pine (*Pinus ponderosa* (Dougl. ex. Loud.)) and communities of grasses and sagebrush where the average annual precipitation is approximately 320 mm. This steep-sided sink is about 13 m deep and 32 m wide by 170 m long (Greeley 1971) and serves as a cold air trap. Thus, the microclimate on the floor of the sink differs markedly from that of the surface. In fact permanent ice is found in Charcoal Cave at the northwestern end of the sink, and the mossy-litter layer inhabited by *A. forbesi* is frozen during most of the winter. Species differ on the two levels. For example, *A. forbesi* and *Syarinus* sp. live in the semi-mesic litter of the sink, while *Dactylochelififer silvestris* Hoff and *Haplochelififer philipi* (Chamberlin) inhabit the semi-xeric litter beneath the ponderosa pine and green manzanita (*Arctostaphylos patula* Greene) of the surface.

Material examined.—Only the types.

ACKNOWLEDGMENTS

The use of research facilities at Malheur Field Station, near Burns, Oregon, is gratefully acknowledged. The holotype and allotype are deposited in the American Museum of Natural History (AMNH).

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RESEARCH NOTES

LOW TEMPERATURE ACTIVITY OF PSEUDOSCORPIONS
AND PHALANGIDS IN SOUTHERN MANITOBA

Horizontal activity of pseudoscorpions and phalangids on the soil surface was determined by means of modified pitfall traps (Aitchison 1974), from October 1973, until May 1975, covering two winter periods with snow cover. In those periods they were collected occasionally. The snow cover acts as a blanket for the soil surface, maintaining the temperature there at close to or just below 0°C while the ambient air temperatures vary between -15° and -35°C. Temperatures under the snow were monitored by thermistor probes in 1973-1974 and by a simple radiotelemetric device in 1974-1975 (Aitchison 1974). The three habitat sites were a ridge between two ponds, an aspen-bur oak wood and a damp meadow; collection and description of the study area are described by Aitchison (1974, 1978).

Two species of pseudoscorpions were collected: *Microbisium brunneum* (Hagen) and *M. confusum* Hoff. Both species are parthenogenetic (Hoff 1949). Five adult females and tritonymphs of *M. brunneum* were collected from the ridge and the meadow: one on 31 October 1973, another on 21 November 1973, when the subnivean (under the snow) temperature was -1.5°C. In the winter of 1974-1975 the three remaining specimens were trapped in November and December at subnivean temperatures ranging between -1° and -4°C. One tritonymph of *M. confusum* was taken at a subnivean temperature of -6°C on 28 March 1974.

Weygoldt (1969) reported that in some parts of Europe *Neobisium muscorum* (Leach) was active throughout the cold season, while some other species of pseudoscorpions were active whenever temperatures exceeded 0°C. Höregott (1963) using pitfall traps found that adult activity in *N. muscorum* occurred from October until March, peaking in December and January. This corroborates the data from southern Manitoba where activity occurred mainly between October and December in a somewhat lower temperature range.

Three species of phalangids were collected: *Odiellus pictus* Wood, *Odiellus* sp. nr. *pictus* Wood and an immature *Leiobunum* sp. A total of five specimens were taken in autumn and spring only, one of which was an adult male *O.* sp. nr. *pictus* collected in mid-October 1973. In 1974-1975 four immatures were trapped in an aspen-bur oak wood on 31 October, 7 November and in May. At the end of October, the soil surface temperature was recorded as -0.6°C; in the first week of November it varied between 0° and 4°C; and in May it was 2°C. No specimens were taken during periods of snow cover. It seems as though harvestmen were limited to activity usually at times when the soil surface temperatures exceeded 10°C.

Todd (1949) explained that the species with which she experimented were able to survive -4° to -4.5°C for one hour and furthermore that -9°C was the critical minimum for *Phalangium opilio* L. In Germany activity in winter months was noted in juveniles of *Oligolophus tridens* Koch and *Platybunus triangularis* Herbst (Höregott 1963). *O. pictus* appeared in this study to be active in the temperature range of -0.6° to 4°C in autumn and spring.

Determinations of pseudoscorpions were kindly done by W. B. Muchmore, University of Rochester, New York, and those of phalangids by C. D. Dondale, Biosystematics Research Institute, Agriculture Canada, Ottawa.

C. W. Aitchison, Department of Entomology, University of Manitoba, Winnipeg, Manitoba R3T - 2N2, Canada.

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A NEW WOLF SPIDER IN THE GENUS *SCHIZOCOSA* (ARANEAE: LYCOSIDAE) FROM ILLINOIS

The purpose of this paper is to describe a new species of *Schizocosa* from specimens collected beside a stream in a central Illinois floodplain forest. These specimens are of particular interest in that the structure of the male palpus and female epigynum are apparently inseparable from those of the widespread eastern species *S. ocreata* (Hentz).

Dondale and Redner (1978, *Canadian Entomol.* 110: 143-181), in a revision of the genus *Schizocosa*, indicated that *S. ocreata* embraces occasional males in which the usually conspicuous brush of erect, black setae on tibia I is reduced or completely absent. Laboratory studies on an Illinois population of "brushless" individuals indicate that it represents a species separable from *S. ocreata* on the basis of a reproductive barrier. Our purpose here is to describe this new species and thus make the name available for use in future publications.

Anatomical terminology follows that of Dondale and Redner (1978).

Schizocosa rovneri, new species

Male.—Total length 6.48 to 8.07 mm. Carapace 3.48 to 4.07 (mean 3.73) mm long and 2.57 to 2.95 (mean 2.77) mm wide (10 specimens measured). Carapace with lateral areas red-brown, streaked with black; pale submarginal bands slender and indistinct, not extending to carapace margins; pale median band wide, with smooth, undulating margins. Sternum dull orange-red. Chelicerae red-brown, setaceous, with 3 teeth on promargin of fang furrow and 3 on retromargin. Legs yellow-orange, paler toward extremities, usually lacking dark rings; leg I not darker than II to IV, without tibial brush. Dorsum of abdomen without heart-mark, with black marginal band along each side, without chevrons. Venter dull red or paler. Cymbium of palpus with approximately 10 stout terminal macrosetae. Median apophysis with distal margin convex and undulating. Embolus with intromittent part slender and pointed, nearly straight but with slight hook ventrad at tip. Palea with long distal process, and with furrow marking off rugose prominence on retrolateral side. Terminal apophysis scale-like, with thickened margin, extending to and concealing base of intromittent part of embolus. (Note: external genitalia as illustrated for *S. ocreata* (Hentz); see Dondale and Redner, 1978).

Female.—Total length 6.01 to 7.95 mm. Carapace 3.45 to 4.28 (mean 3.91) mm long and 2.64 to 3.24 (mean 2.93) mm wide (7 specimens measured). General structure and color essentially as in male. Epigynum with moderately deep atrium; median septum with longitudinal piece broad posteriorly and narrowing anteriorly, with slightly concave, slightly irregular lateral margins; transverse piece with large, paired surface excavations having distinct margins, these excavations nearly meeting at mid-line. Spermathecae ovoid, smooth, separated by approximately their width. (Note: external genitalia as described for *S. ocreata* (Hentz) by Dondale and Redner (1978) figs. 36-38).

Type material.—Holotype male from Allerton Park, Piatt Co., Illinois, 22 May 1973, deposited in the American Museum of Natural History, New York, N.Y. Ten male and 6 female paratypes from the type locality, dated either 22 or 16 May 1973, deposited in the Canadian National Collection of Insects and Arachnids, Ottawa, Ont.

Comments.—Individuals of *S. rovneri* are anatomically indistinguishable from those of *S. ocreata* (Hentz) except by the lack of tibial brush on leg I of the male. Both sexes key to *ocreata* in Dondale and Redner's key to species, and respective carapace dimensions fall within one standard deviation of the means given by those authors for *ocreata*. Males resemble those of *S. floridana* Bryant in lacking a tibial brush, but differ in having a rugose (rather than smooth) prominence marked off the palea of the genital bulb of the palpus; females also resemble those of *floridana* in general, but are separable by the closely-set surface excavations in the transverse piece of the epigynal septum.

Individuals of *rovneri* clearly differ from those of *ocreata* in sexual behavior. Laboratory studies of courtship indicate that males of *rovneri* approach the female and court in qualitatively and quantitatively different ways. Females of both species were courted equally well, but in no instance did the *ocreata* female permit a *rovneri* male to mount and copulate. When males of *ocreata* were placed with females of *rovneri*, they courted but were not permitted to mount and copulate. Conspecific matings for both species in the same tests proceeded normally and resulted in egg deposition and hatching. The behavioral data will be published in full elsewhere.

S. rovneri is named in honor of Dr. J. S. Rovner in recognition of his stimulating work on the behavior of North American wolf spiders. This research was supported in part by funds provided by the University of Cincinnati Research Council.

George W. Uetz, Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221, U.S.A., and Charles D. Dondale, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario KIA OC6, Canada.

APPARENT ATTRACTION OF MOTHS BY THE WEBS OF ARANEID SPIDERS

This preliminary note concerns observations of apparent attraction of prey by three species of araneids: *Argiope aurantia* Lucas, *Argiope trifasciata* (Forsk.) and *Araneus trifolium* (Hentz). The prey species involved was the day-flying saturniid moth, *Hemileuca lucina* Edwards (Northern Buckmoth).

The observations were made during a study of a dense population of *H. lucina* in Worcester County, Massachusetts during middle and late September 1977. The population was located within a power-line cut which resembled a moist old field habitat (some shrubs and small trees were present). On 18 September I was in the study area during the flight period of the moths, and it was apparent that male moths were being attracted to the webs of the spiders in some way. I observed as many as six males simultaneously hovering around a given spider's web, and on occasion a moth would become ensnared. The hovering behavior of the moths differed from their normal flight. During normal flight the movement of the moths in the air was somewhat erratic, but with a clear forward component. During the hovering flight the forward component was largely lacking, and the moths tended to remain in one place. On three occasions I also observed moths hovering around partially destroyed webs which contained no spiders. These last observations suggest that whatever attracted the moths emanated from the web.

Attraction of potential prey has been recorded for a bolas spider, *Mastophora* sp., by Eberhard (1978, Science 198: 1173-1175). Eberhard's observations indicated that the attraction was probably due to a mimic of a sex attractant of the noctuid moth, *Spodoptera frugiperda*. He observed that only male moths were attracted, and that their approach to the spider was from down wind.

It is not clear at this point whether the attraction of prey which I observed was due to a chemical or a visual factor. The fact that only male moths were observed hovering suggests a sex attractant mimic as in the case of *Mastophora*. However, records from the morning of 18 September indicated that the resting population of moths was about 94% males (N=214). Male buckmoths also spend more time in flight than do the females.

Charles C. Horton, Department of Zoology, Morrill Science Center, University of Massachusetts, Amherst, MA 01003, U.S.A.

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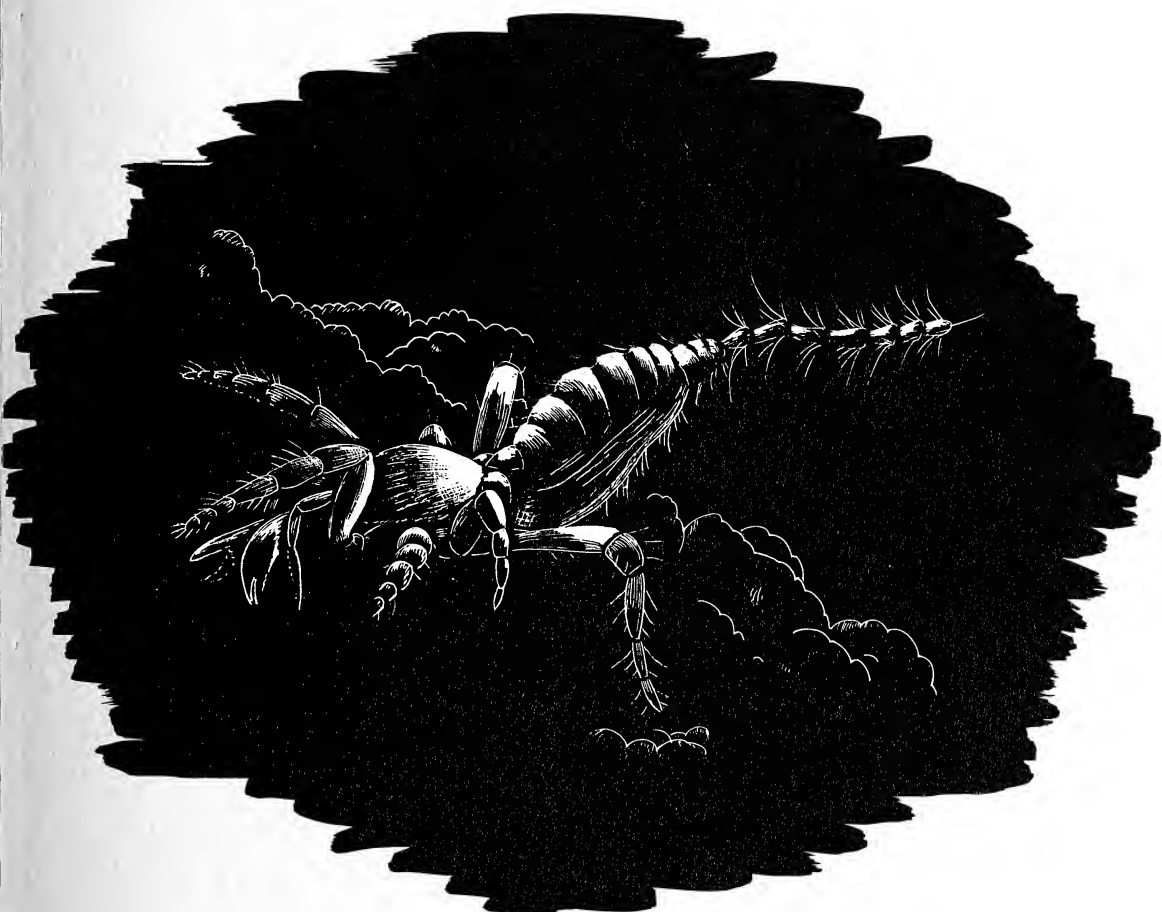
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THE ORDER SCHIZOMIDA (ARACHNIDA) IN THE NEW WORLD. II. *SIMONIS* AND *BRASILIE*NSIS GROUPS (SCHIZOMIDAE: *SCHIZOMUS*)¹

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ABSTRACT

A systematic revision of the *Schizomus simonis* and *S. brasiliensis* species groups (Arachnida, Schizomida, Schizomidae) is presented. The following species are described and assigned to the *simonis* group: *S. drakos* n. sp., *S. simonis* Hansen, *S. trinidadus* n. sp., *S.acrocaudatus* n. sp., *S. flavescens* Hansen, *S. tobago* n. sp., *S. mumai* n. sp., and *S. centralis* Gertsch. Two taxa known only from females (*Schizomus* spp., OTU Nos. 1 and 2) are also briefly described and assigned to the *simonis* group. The following species are described and assigned to the *brasiliensis* group: *S. stewarti* Rowland, *S. trilobatus* Rowland, *S. lacandonus* Rowland, *S. cuenca* n. sp., *S. sturmi* (Kraus), *S. brasiliensis* (Kraus), *S. macarensis* (Kraus), *S. cumbalensis* (Kraus), and *S. pallipatellatus* n. sp. Brief descriptions are also provided for six taxa assigned to the *brasiliensis* group that are known only from females (*Schizomus* spp., OTU Nos. 7-12).

INTRODUCTION

This is the second in a series of systematic reports revising the arachnids of the order Schizomida in the New World. The first report (Rowland and Reddell 1979) covered the family Protoschizomidae and the *Schizomus dimitrescoae* group of the family Schizomidae. The present report includes a revision of two primarily South American species groups of the family Schizomidae, the *Schizomus simonis* and *S. brasiliensis* groups. Uniform descriptions are included for previously described species as well as for new species, and include all characters which have been found to be of value in distinguishing taxa (see Rowland and Reddell 1979, for a discussion of the characters used). Table 1 may be used to compare the species groups included here with the remaining groups of New World schizomids. Future reports will revise the remaining species groups of New World schizomids and discuss in detail the zoogeography and phylogeny of the order in the New World.

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Several species are described in this report for which males are not available. These taxa are not named, but are included because they are of value in analyzing the phylogenetic and zoogeographic relationships within the order. As we earlier discussed (Rowland and Reddell 1979), the formal taxonomic recognition of species of schizomid known only from females is unwise, since the only completely reliable characters for the recognition of species are the flagellum and secondary sexual characters of males. The females briefly described and illustrated in the present study are certainly distinct taxa as based on study of the spermathecae, but variation in this character is too great to guarantee that specimens from nearby localities could be accurately identified. These taxa are referred to as Operational Taxonomic Units (OTU's) for purposes of phylogenetic and zoogeographic analysis.

Table 1.--Comparisons of the New World species groups of the genus Schizomus. See Rowland and Reddell (1979) for explanation of characters.

CHARACTER	dumitres- coae	simonis	brasil- iensis	mexi- canus	pecki	goodni- ghtorum	briggsi
DORSAL SETAE	2-3	2-3	3-4	2-3	2-3	3-4	3-4
METAPEL- TIDIUM	entire	entire	split or entire	entire	entire	entire	split or entire
COLOR	brown or green	brown or green	brown or green	brown or green	brown	brown	brown or green
SPERMA- THECAE	M < L	M < L	M = L	M > L	M > L	M > L	multiple
ART. FEM. FLAGELLUM	4	4	3	3	3	3	4
CARAPACE LENGTH	.96-1.37	1.07-1.34	.91-1.48	.98-1.37	1.31-1.74	.89-1.42	1.18-1.52
ABDOMINAL ELONGATION	none	present	none	none	none	present	none or present
ABDOMINAL PROCESS	present	present	present	absent	absent	absent	present
PEDIPALPAL DIMORPHISM	slight to strong	none	slight to strong	none to strong	none	none	none to strong
SHAPE MALE FLAGELLUM	bulbous	long	bulbous	bulbous	bulbous	long	long or bulbous

The present study is based to a large extent on a dissertation prepared by the senior author at Texas Tech University, Lubbock, Texas (Rowland 1975a).

Family Schizomidae

SIMONIS GROUP

Description.—Members of this group are characterized by moderate to great length (1.07-1.34 mm carapacial length). Color is brownish. Eyespots are present, but are usually indistinct. The carapace has two to three pairs of dorsal and two apical setae. Males: abdomen attenuate, the elongation either limited to the pygidial segments or involving segments V-XII; abdominal segment XII with a posterodorsal process, which is usually truncate, but in a few species is rounded; flagellum longer in species with elongated abdomen, but shorter in species with lesser attenuation; a pair of subproximal flagellar elevations, often undercut, present in all species. Females: Flagellum 0.37 to 0.61 mm in length, composed of four articles; spermathecae characterized by elongation of lateral pair, and usually a slight reduction of median pair; apex of the spermathecae, at least of the lateral pair, with sclerotized bulbs. The pedipalps are not sexually dimorphic.

Distribution.—Central America: Costa Rica, Panama. South America: Venezuela, Trinidad, Tobago, British Guiana.

Remarks.—Species which may belong to this group, but which have not been examined include *S. gladiator* Remy, 1961, *S. surinamensis* Remy, 1961, and *S. vanderdrifti* Remy, 1961, from Surinam; and *S. dispar* Hansen (*in* Hansen and Sørensen 1905) from Martinique. Table 2 gives characters used in separating the species of the *simonis* group.

Subordinate taxa.—*Drakos* complex: OTU No. 1, OTU No. 2, *S. drakos* n. sp.; *simonis* complex: *S. simonis* Hansen, *S. trinidadus* n. sp., *S. acrocaudatus* n. sp., *S. flavescens* Hansen; *centralis* complex: *S. tobago* n. sp., *S. mumai* n. sp., *S. centralis* Gertsch.

Schizomus sp., OTU No. 1

(Figs. 1, 21)

Description.—Female. Color brownish. Carapace with three pairs of dorsal setae, the middle pair smallest, and two apical setae. Eyespots indistinct. Anterior sternum with 10 bifid setae, posterior sternum with bifid setae. Abdominal terga I-VIII with two setae, tergum IX with four setae. Vestigial stigmata darker than sterna. Flagellum missing. Pedipalpal trochanter not produced apically; tarsal-basitarsal spur about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 33-4-6-7-7-7-17. Other leg segment measurements given in Table 3. Median and lateral spermathecae about same size; wide basally to apically; no localized sclerotization; laterals bent outward basally; medians convergent, laterals divergent.

Male unknown.

Specimen examined.—Female taken at Atkinson Field, British Guiana, 8 November 1959 (collector unknown) (AMNH).

Distribution.—Known only from Atkinson Field, British Guiana.

Remarks.—This species is most closely related to *Schizomus* sp., OTU No. 2, with which it shares a unique development of the spermathecae. It is best distinguished from OTU No. 2 by its lack of a sclerotized basal portion under the spermathecae.

Schizomus sp., OTU No. 2
(Figs. 1, 19-20)

Description.—Female. Color brownish. Carapace with three pairs of dorsal setae, the middle pair smallest, and two apical setae. Eyespots indistinct. Anterior sternum with 11 bifid setae, posterior sternum with bifid setae. Abdominal terga I-VIII with two setae, tergum IX with four setae. Vestigial stigmata darker than sterna. Flagellum with four sections. Pedipalpal trochanter not produced distally; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 35-5-8-8-8-17. Other leg segment measurements given in Table 3. Median and lateral spermathecae similar in shape, but laterals longer; both pair wide basally, slightly narrower apically, ending in a small cleft; no special sclerotization; medians convergent, laterals divergent; medians and laterals basally connected to a basal piece.

Male unknown.

Specimens examined.—Female taken in the Bartica District, British Guiana, 6 May 1924 (collector unknown) (AMNH); two females taken in Kartabo 1, British Guiana, 1919 (A. Emerson) (AMNH).

Distribution.—Known only from Bartica District and Kartabo 1, British Guiana.

Table 2.—Comparisons of members of the *simonis* group. See the introduction to Rowland and Reddell (1979) for discussion of characters.

CHARACTER	OTU #1	OTU #2	drakos	simonis	flave- scens	acroca- udatus	trini- danus	tobago	mumai	centralis
DORSAL SETAE	3	3	3	2	2	2	2	2	2	2
STERNAL SETAE	10	11	12	11	11	10	11	11	11	11
ABDOMINAL PROCESS	?	?	round	round	?	small truncate	medium truncate	small truncate	large truncate	large truncate
EYESPOTS	indis- tinct	indis- tinct	indis- tinct	indis- tinct	indis- tinct	indis- tinct	distinct	indis- tinct	distinct	distinct
SPERMA- THECAE	L=M	L=M	?	multiple	L=M	?	L=M	L=M	L 2X M	L ± M
CARAPACE LENGTH	1.08	1.29	1.34	1.40	1.33	1.14	1.14	1.12	1.14	1.12
LENGTH FEM. FLAGELLUM	?	.38	?	.52	.61	?	.37	.41	.40	.37
ABDOMINAL ELONGATION	?	?	5-12	10-12	?	7-12	10-12	7-12	5-12	7-12
ELEV. MALE FLAGELLUM	?	?	present	present	?	present	present	absent	present	absent
PIT MALE FLAGELLUM	?	?	double	double	?	double	double	single	single	single

Table 3.—Measurements (mm) of species of the *simonis* group: 1, one female, OTU No. 1; 2, one female, OTU No. 2; 3, one male, *S. drakos*; 4, one male, *S. simonis*; 5, one female, *S. simonis*; 6, three males, *S. trinidadus*; 7, three females, *S. trinidadus*; 8, one female, *S. flavescens*. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6	7	8
Carapace	1.08	1.29	1.34	0.95	1.40	1.07-1.07	1.11-1.14	1.33
Flagellum								
Length	-	0.38	0.58	0.40	0.52	0.43-0.45	0.37-0.40	0.61
Width	-	-	0.38	0.19	-	0.22-0.23	-	-
Leg I								
Femur	1.11	1.17	1.78	1.15	1.40	1.03-1.10	1.02-1.05	1.48
Patella	1.30	1.41	2.24	1.44	1.68	1.28-1.35	1.25-1.28	1.78
Tibia	0.96	1.06	1.64	1.06	1.22	0.93-0.97	0.93-0.93	1.43
Tarsus-basitarsus	0.80	0.89	1.14	0.86	1.00	0.79-0.82	0.78-0.78	1.08
Leg II								
Femur	0.75	0.82	1.04	0.65	0.96	0.67-0.71	0.70-0.72	1.00
Patella	0.42	0.49	0.53	0.33	0.50	0.39-0.40	0.41-0.44	0.61
Tibia	0.45	0.50	0.65	0.40	0.55	0.39-0.43	0.42-0.43	0.65
Basitarsus	0.43	0.44	0.56	0.40	0.56	0.36-0.38	0.37-0.37	0.54
Leg III								
Femur	0.66	0.70	0.86	0.56	0.42	0.58-0.60	0.61-0.62	0.87
Patella	0.31	0.35	0.37	0.23	0.40	0.25-0.26	0.28-0.29	0.42
Tibia	0.35	0.39	0.49	0.26	0.41	0.30-0.32	0.30-0.32	0.45
Basitarsus	0.45	0.47	0.63	0.40	-	0.35-0.36	0.37-0.40	0.56
Leg IV								
Femur	1.06	1.14	1.41	1.00	1.32	0.95-0.99	0.97-1.06	0.89
Patella	0.46	0.55	0.58	0.36	0.65	0.44-0.47	0.47-0.52	0.40
Tibia	0.71	0.79	0.93	0.65	0.89	0.61-0.63	0.64-0.67	0.49
Basitarsus	0.64	0.70	0.90	0.53	0.83	0.54-0.57	0.55-0.58	0.54

Variation.—The spermathecae of the three specimens examined show some marked differences. In the specimen from the Bartica District the medians are smaller than the laterals and the basal portion is smaller than either pair of spermathecae. The spermathecae of the Kartabo 1 specimens are larger and the medians and laterals are more clearly equal in size, although there is a marked asymmetry in the size of the laterals; and the basal portion of the spermathecae is larger than either the laterals or medians.

Remarks.—It is possible that these two collections represent different, though closely related species. Without males or additional females from these and other localities, however, it is more convenient to consider them as representatives of a single species.

Schizomus drakos, new species
(Figs. 1, 4)

Description.—Male. Color brownish. Carapace with three pairs of similar dorsal and two apical setae. Eyespots oval, indistinct. Anterior sternum with 12 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; abdominal segments V-XII extremely elongate; segment XII with rounded posterodorsal process. Vestigial stigmata darker than sterna. Flagellum nearly triangular, with a pair of median pits flanked proximally by a pair of lateral swellings. Pedipalpal trochanter not produced

distally; tarsal-basitarsal spurs about $1/5$ length of tarsus-basitarsus, claw missing. Tarsal-basitarsal segments of leg I of the following approximate proportions: 49-6-9-10-8-11-21. Other leg segment measurements given in Table 3.

Female unknown.

Type data.—Holotype male taken in Kartabo, Bartica District, British Guiana, 12 October 1920 (collector unknown) (AMNH).

Comparisons.—This species appears to be closely related to OTU Nos. 1 and 2, based on the general morphology, although comparison is difficult due to the absence of a female of *S. drakos* and males of the other two species. It may be readily distinguished from OTU Nos. 1 and 2, however, by the presence of four setae on terga VIII in *S. drakos* and two setae on terga VIII of OTU Nos. 1 and 2. *S. drakos* may be separated from other species of the *simonis* group by the presence of three pairs of dorsal setae, while all other *simonis* group species possess only two pairs.

Distribution.—Known only from the type locality.

Etymology.—*Drakos* is from the Greek word meaning dragon, a name inspired by the elongate abdomen of this species.

Schizomus simonis Hansen
(Figs. 1, 6, 13, 28-29)

Schizomus simonis Hansen (in Hansen and Sørensen) 1905:5, 7, 14, 15, 19, 22, 24, 38, 39, 42-44, 71-73; Chamberlin 1922:12; Mello-Leitão 1931:19; Giltay 1935:7; Gertsch 1940:3; Takashima 1943:93; Remy 1961:504; Lawrence 1969:219, 221, 223.

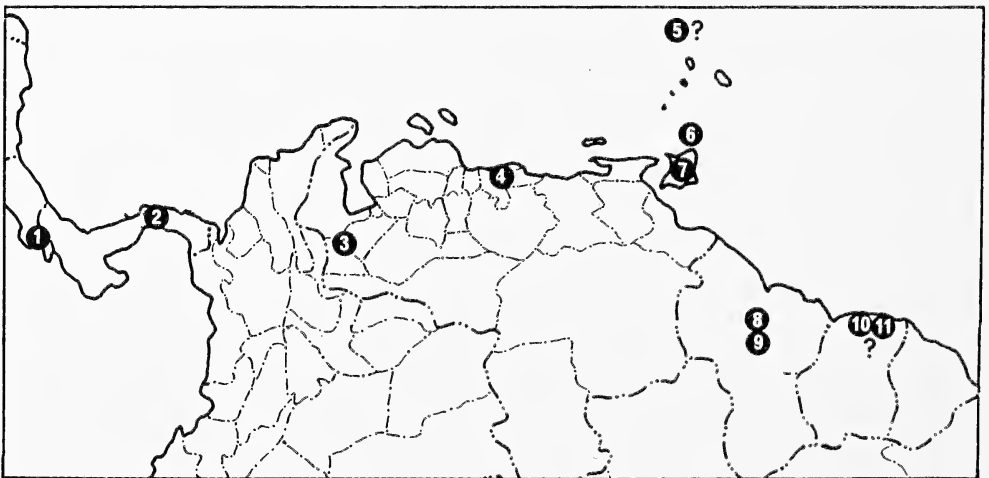


Fig. 1.—Map showing distribution of schizomids of the *simonis* group: 1, *S. mumai*; 2, *S. centralis*; 3, *S. simonis*; 4, *S. flavescens*; 5, *S. dispar*; 6, *S. tobago*; 7, *S. trinidadus*, *S.acrocaudatus*; 8, *S. drakos*; 9, OTU No. 1, OTU No. 2; 10, *S. gladiator*; 11, *S. vanderdrifti*, *S. surinamensis*. Question marks indicate species doubtfully placed in the *simonis* group.

Description.—Male. Color greenish. Carapace with two pairs of dorsal and two apical setae. Eyespots oblong, indistinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; abdominal segments X-XII elongate, tapering, segment XII with slight development of posterodorsal process. Vestigial stigmata nearly indistinguishable from sterna. Flagellum extended distally, apex acute; dorsal surface with two lateral swellings distally undercut by lateral pits. Pedipalpal trochanter produced very slightly; tarsal-basitarsal spurs about $1/6$, claw about $1/4$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 33-5-6-7-9-8-14. Other leg segment measurements given in Table 3.

Female. Abdomen not elongate. Flagellum with four articles. Six to eight pairs of spermathecae of varying size.

Type data.—Cotypes: male taken at St. Esteban, Venezuela, by E. Simon (UZMK, examined); female (UZMK, examined) and male and female (NRS, examined), taken at Colonia Tovar, Venezuela, by E. Simon.

Comparisons.—See under *S. trinidadus* and *S.acrocaudatus*.

Distribution.—Known only from Colonia Tovar and St. Esteban, Venezuela.

Remarks.—The morphology of the female spermathecae in this species is unique within the *simonis* group, but it is possible that the female of this species has been misassociated with the male and that this is the female of another species. This may also be indicated by the difference in leg measurements between males and females which in other species of schizomids are usually the same or very similar in both sexes.

Variation.—The male flagellum as figured by Hansen (*in* Hansen and Sörensen 1905) is much longer than that of the cotype examined in this study.

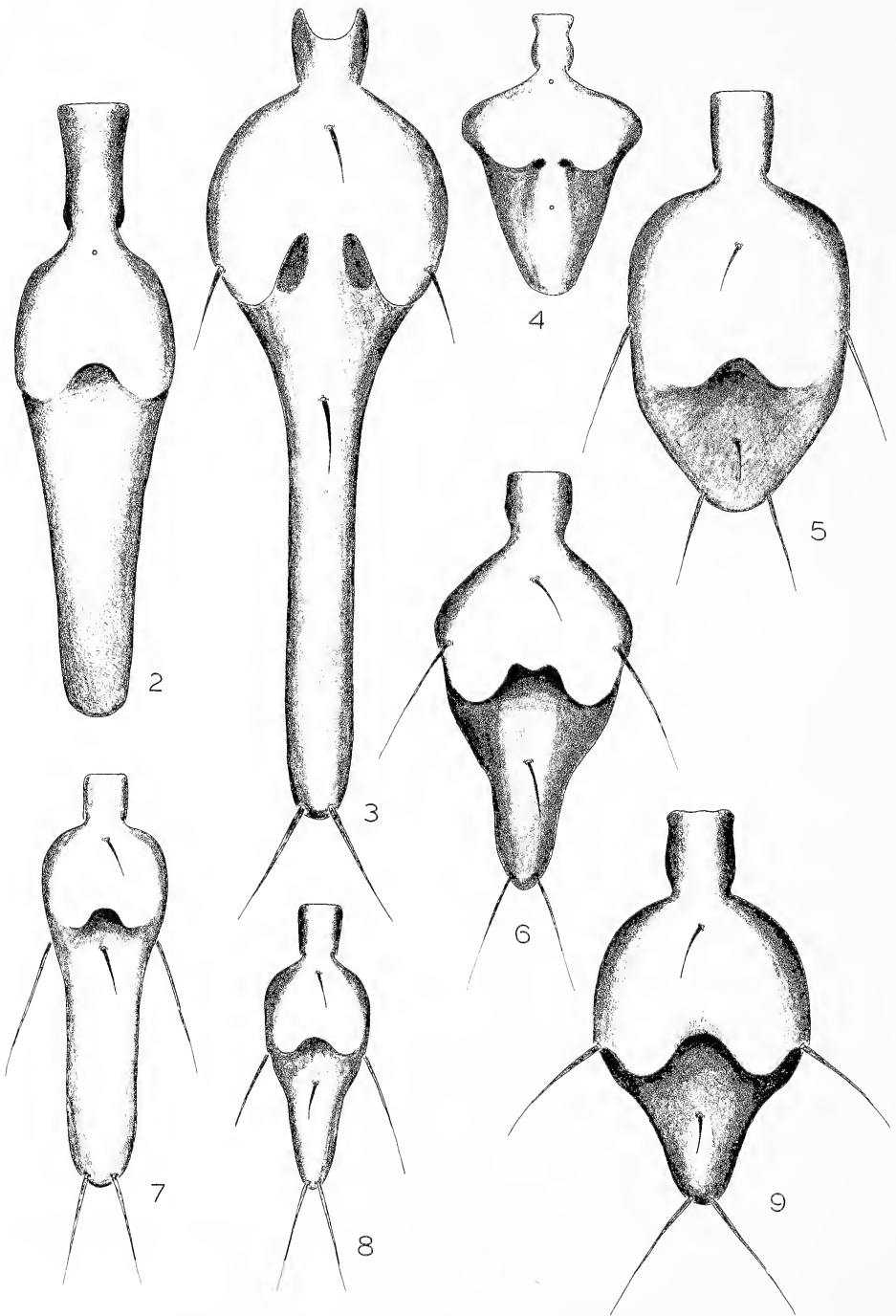
Schizomus trinidadus, new species
(Figs. 1, 9, 14, 16, 31-33)

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots irregular, distinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; abdominal segments X-XII slightly elongate, segment XII with truncate posterodorsal process. Vestigial stigmata darker than sterna. Flagellum lanceolate, with a pair of median depressions flanked proximally by pair of lateral swellings. Pedipalpal trochanter not produced apically; tarsal-basitarsal spurs about $1/4$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 30-5-6-6-7-7-11. Other leg segment measurements given in Table 3.

Female. Abdomen not elongate. Flagellum with four articles. Lateral and median spermathecae short, nearly equal in size, terminating in slight sclerotized bulbs.

Type data.—Holotype male, allotype female, paratype male and eight paratype females, taken in Arima Valley, Trinidad (8-1200 ft.), 10-22 February 1964 (P. Wygodzinsky) (MCZ).

Comparisons.—Males of *S. trinidadus*, like *S. simonis*, have only the pygidial segments of the abdomen elongate. The shape of the male flagellum is similar in the two species, but is somewhat more elongate in *S. simonis*. The eyespots are also more distinct in *S. trinidadus* and the posterior abdominal process is truncate in *S. trinidadus*, whereas it is round in *S. simonis*. If the female of *S. simonis* is correctly assigned, it may readily be distinguished from that of *S. trinidadus* in having multiple spermathecae rather than only



Figs. 2-9.—Dorsal views of male flagella of the *simonis* group: 2, *S. tobago*; 3, *S.acrocaudatus*; 4, *S. drakos*; 5, *S. centralis*; 6, *S. simonis*; 7-8, *S. mumai*; 9, *S. trinidanus*.

two pairs. The single dorsal depression in the male flagellum and the long spermathecae of *S. tobago* readily separates it from *S. trinidadus*. The male of *S.acrocaudatus*, which was collected with types of *S. trinidadus*, can be distinguished by the much longer flagellum and elongate abdomen involving abdominal segments VII-XII. Unknown variability in the latter characters, however, may leave the deep dorsal depressions on the flagellum as being a more useful character in distinguishing these two species.

Distribution.—Known only from Arima Valley, Simla, and St. Augustine, Trinidad.

Etymology.—The specific name is an adjectival form of Trinidad.

Variation.—The morphology of the spermathecae is fairly consistent throughout the range of the species. The specimen from Arima Valley has slightly less distinct apical bulbs, apparently because they are somewhat thicker basally. The three males from St. Augustine show only very slight elongation of the pygidial abdominal segments. This variation in secondary sexual characteristics is also known in other species.

Additional records.—Trinidad: Simla, bamboo debris, 26 April 1964 (Chickering), 5 females (MCZ); 23 April 1964 (Chickering), 1 female (MCZ); 18 April 1964 (Chickering), 2 females (MCZ); 20-21 April 1964 (Chickering), 1 female (MCZ); 25 April 1964 (Chickering), 2 females (MCZ); 16 April 1964 (Chickering), 5 females (MCZ); 28 April 1964 (Chickering), 4 females (MCZ); 12 April 1964 (Chickering), 3 females (MCZ); 19 April 1964 (Chickering), 3 females (MCZ). Arima Valley (8-1200 ft.), 10-22 February 1964 (J. Rozen, P. Wygodzinsky), 6 females, 2 immatures (AMNH). St. Augustine, date unknown (Weber), 3 males, 10 females (MCZ).

Schizomusacrocaudatus, new species
(Figs. 1, 3, 12)

Description.—Male. Color brownish. Carapace (length 1.14 mm) with two pairs of dorsal and two apical setae. Eyespots irregular, indistinct. Anterior sternum with 10 setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; abdominal segments VII-XII slightly elongate, segment XII with small, truncate posterodorsal process. Vestigial stigmata darker than sterna. Flagellum extremely long and distally very thin, with a pair of median deep pits flanked laterally by pair of swellings; length, 0.86 mm, width, 0.29 mm. Pedipalpal trochanter not produced distally; tarsal-basitarsal spurs about 1/5, claw about 1/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I missing.

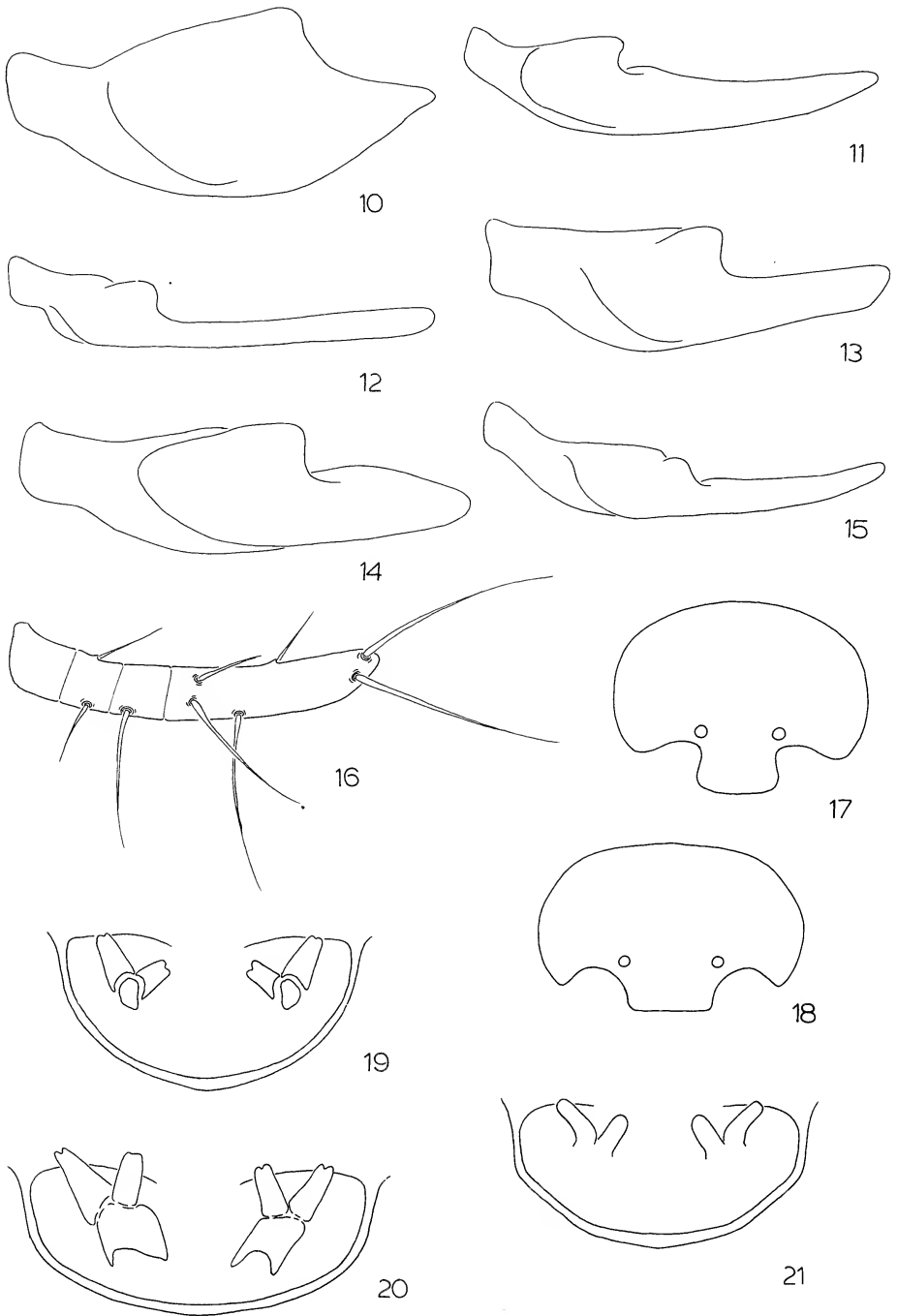
Female unknown.

Type data.—Holotype male taken at St. Augustine, Trinidad, date unknown (M. A. Weber) (MCZ).

Comparisons.—*S.acrocaudatus* is very similar to *S. simonis* in development of the male flagellum. The male cotype of *S. simonis* illustrated by Hansen (in Hansen and Sörensen 1905), though not the cotype available to us, shows the flagellum to be very similar to that of *S.acrocaudatus*. The attenuation of the abdomen, however, involves segments VII-XII in *S.acrocaudatus* but only segments X-XII in *S. simonis*. The flagellum of *S.acrocaudatus* is much thicker basally and the pair of dorsal depressions are visible from directly above, while in *S. simonis* the male flagellum is flatter dorsally and the pair of depressions are not clearly visible from above. The posterodorsal abdominal process is round in *S. simonis* and truncate in *S.acrocaudatus*.

Distribution.—Known only from the type locality.

Etymology.—The specific name is taken from the Latin *acr-* meaning sharp and *caud-* meaning tail, describing the morphology of the male flagellum.



Figs. 10-21.—Parts of schizomids of the *simonis* group: 10-15, lateral views of male flagella: 10, *S. centralis*; 11, *S. mumai*; 12, *S.acrocaudatus*; 13, *S. simonis*; 14, *S. trinidanus*; 15, *S. tobago*; 16, lateral view of female flagellum of *S. trinidanus*; 17-18, dorsal views of male posterodorsal abdominal process: 17, *S. centralis*; 18, *S. mumai*; 19-21, female spermathecae: 19-20, OTU No. 2; 21, OTU No. 1.

Remarks.—As in other species with an elongate abdomen and flagellum, the degree of attenuation can be highly variable. It is more reliable to use the basal configuration of elevations and depressions in distinguishing species with elongate abdomens and flagella.

Schizomus flavescens Hansen

(Figs. 1, 27)

Schizomus flavescens Hansen (in Hansen and Sörensen) 1905:44-46, 47, 73; Mello-Leitão 1931:17; Hilton 1933:92; Giltay 1935:6; Takashima 1943:93.

Description.—Female. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata not distinguishable from sterna. Flagellum with four articles, extremely long. Pedipalpal trochanter produced slightly distally; tarsal-basitarsal spurs about $1/4$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 43-8-7-8-9-11-22; other leg segment measurements given in Table 3.

Male unknown.

Type data.—Cotypes: Female (ZMK, examined), two females and an immature (MNHN), taken at Corosul, near Caracas, Venezuela, date unknown (E. Simon); female taken at Corosul, 1888 (E. Simon) (NRS, examined).

Comparisons.—The female of this species is easily distinguished from other species of the *simonis* group by the extremely long flagellum. The species most closely approaching *S. flavescens* in length of the female flagellum is *S. simonis* (0.52 mm as opposed to 0.61 mm in *S. flavescens*). The morphology of the spermathecae is most similar to, and perhaps not distinguishable from, *S. tobago* and *S. centralis*. The extremely long first legs will, however, distinguish *S. flavescens* from *S. tobago*.

Distribution.—Known only from the type locality.

Remarks.—Hansen (in Hansen and Sörensen 1905) reports that *S. flavescens* is very similar to *S. dispar*. The latter species, however, was unavailable for study.

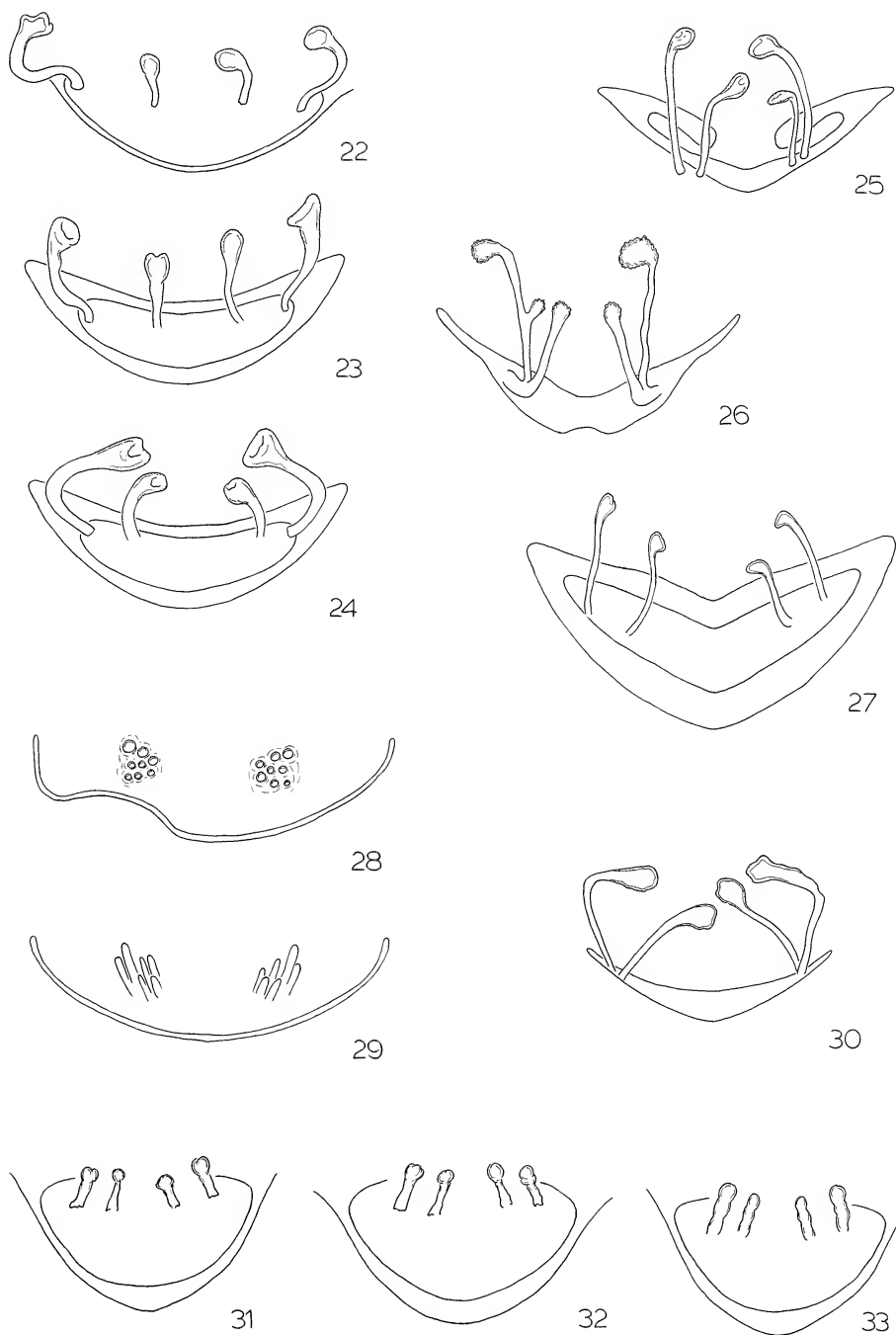
Schizomus tobago, new species

(Figs. 1-2, 15, 30)

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segments VII-XII elongate, segment XII with slight truncate posterodorsal process. Vestigial stigmata not distinguishable from sterna. Flagellum elongate, lanceolate, with a single median depression undercutting a pair of lateral ridges. Pedipalpal trochanter produced slightly apically; tarsal-basitarsal spurs about $1/5$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 36-6-7-7-8-8-18; other leg segment measurements given in Table 4.

Female. Abdomen not elongate. Flagellum composed of four articles. Spermathecae nearly equal in size, long, terminating in sclerotized bulbs.

Type data.—Holotype male and allotype female taken on Tobago, April 1916, by Thomas M[ortensen] (UZMK).



Figs. 22-33.—Female spermathecae of the *simonis* group: 22-24, *S. mumai*: 22, from Golfito; 23-24, from the type locality; 25-26, *S. centralis*; 27, *S. flavescens*; 28-29, *S. simonis*: 28, view from above the perpendicular; 29, view from the perpendicular; 30, *S. tobago*; 31-33, *S. trinidanus*: 31, from St. Augustine; 32, from Simla; 33, from the type locality.

Table 4.—Measurements (mm) of species of the *simonis* group: 1, one male, *S. tobago*; 2, one female, *S. tobago*; 3, two males, *S. mumai*; 4, three females, *S. mumai*; 5, three males, *S. centralis*; 6, five females, *S. centralis*. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6
Carapace	1.23	1.12	1.07-1.24	1.07-1.14	0.92-1.10	1.03-1.12
Flagellum						
Length	0.79	0.41	0.59-0.87	0.39-0.41	0.44-0.45	0.35-0.37
Width	0.22	-	0.23-0.23	-	0.25-0.25	-
Leg I						
Femur	1.32	1.00	1.05-1.34	0.91-0.94	1.00-1.28	0.89-0.98
Patella	1.67	1.23	1.31-1.72	1.10-1.15	1.22-1.65	1.05-1.15
Tibia	1.25	0.89	0.96-1.23	0.83-0.85	0.91-1.15	0.81-0.84
Tarsus-basitarsus	0.90	0.72	0.84-0.95	0.76-0.77	0.82-0.93	0.70-0.76
Leg II						
Femur	0.77	0.65	0.68-0.83	0.65-0.67	0.63-0.80	0.58-0.69
Patella	0.40	0.41	0.41-0.51	0.40-0.41	0.37-0.47	0.38-0.42
Tibia	0.52	0.40	0.44-0.58	0.42-0.44	0.39-0.53	0.38-0.40
Basitarsus	0.43	0.35	0.37-0.46	0.35-0.38	0.35-0.36	0.34-0.38
Leg III						
Femur	0.68	0.61	0.59-0.72	0.59-0.61	0.55-0.65	0.58-0.60
Patella	0.31	0.27	0.26-0.35	0.25-0.28	0.25-0.35	0.26-0.28
Tibia	0.37	0.30	0.30-0.38	0.32-0.33	0.28-0.36	0.28-0.31
Basitarsus	0.43	0.36	0.37-0.44	0.34-0.37	0.34-0.40	0.35-0.38
Leg IV						
Femur	1.09	0.93	0.93-1.03	0.89-0.93	0.93-1.06	0.91-0.96
Patella	0.55	0.45	0.49-0.58	0.43-0.48	0.46-0.52	0.45-0.49
Tibia	0.69	0.61	0.64-0.76	0.63-0.65	0.60-0.75	0.59-0.65
Basitarsus	0.58	0.54	0.55-0.69	0.54-0.55	0.52-0.65	0.53-0.56

Comparisons.—*S. tobago* is similar to *S. mumai* and *S. centralis* in having a single median depression on the male flagellum. The flagellum of *S. tobago*, however, is somewhat more elongate than that of *S. mumai* and much more so than that of *S. centralis*. *S. tobago* may be readily distinguished from *S. simonis* and *S. trinidadus*, which also have elongate flagella, by the presence of one rather than two depressions on the flagellum. The female spermathecae in *S. tobago*, *S. flavescens*, and *S. centralis* are all very similar and perhaps not distinguishable. The lateral spermathecae of *S. mumai* are twice as long as the medians, whereas in *S. tobago* they are about equal in length.

Distribution.—Known only from the type locality.

Etymology.—The specific name is a noun used in apposition.

Schizomus mumai, new species
(Figs. 1, 7-8, 11, 18, 22-24)

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots irregular, but distinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with well-developed, truncate posterodorsal process, segments V-XII elongate. Vestigial stigmata slightly darker than sterna. Flagellum elongate, with a median depression flanked by a

pair of proximal elevations. Pedipalpal trochanter slightly produced distally; tarsal-basitarsal spurs about 1/7, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 45-7-7-7-9-20; other leg measurements given in Table 4.

Female. Abdomen not elongate. Flagellum composed of four articles. Lateral spermathecae about twice as long as medians, both pairs terminating in sclerotized bulbs, the laterals being much the larger.

Type data.—Holotype male and paratype male, 28 June 1957; allotype female, 11 September 1957; two paratype females, 19 July 1957; two paratype females, 19 July 1957; two paratype females, 13 June 1957; paratype female, 4 September 1957, all taken at Coto, Costa Rica (E. Dixon); paratype female taken at Golfito, Costa Rica, 17 September 1957 (E. Dixon). All specimens deposited in the AMNH.

Comparisons.—*S. mumai* is most similar to *S. centralis* in both sexes. Abdominal attenuation, although somewhat variable, involves segments V-XII in *S. mumai*, but only segments VII-XII are attenuated in *S. centralis*. The flagellum of *S. mumai* is much longer and more attenuate than that of *S. centralis*. The flagellar lateral swellings are well defined in *S. mumai*, while they are undeveloped in *S. centralis*. The spermathecae of these two species are also similar, but the laterals are twice as long as the medians in *S. mumai* and only slightly longer than the medians in *S. centralis*. The abdominal attenuation of the males of *S. mumai* serves to distinguish this species from all others within its range. Females of *S. mumai* are similar to *S. dumitrescoae* Rowland and Reddell, which is also known from Costa Rica, but the latter species possesses four pairs of dorsal carapacial setae as opposed to two in *S. mumai*.

Distribution.—Known only from Coto and Golfito, Costa Rica.

Etymology.—This species is named for Martin H. Muma, who first recognized this species as distinct from existing taxa, in recognition of his many contributions to the study of many groups of arachnids including the Schizomida.

Variation.—The flagellum of the holotype is much longer than that of the single male paratype, but is very similar in the shape of the basal portion of the flagellum and in general morphology.

The female spermathecae show considerable variation even at the same locality. The sclerotized bulbs all are approximately similar, but the spermathecal tubes vary in their configuration.

Schizomus centralis Gertsch
(Figs. 1, 5, 10, 17, 25-26)

Schizomus centralis Gertsch 1941:13-14.

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots oval, distinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segments VII-XII elongate, tapering; segment XII with well-developed, truncate posterodorsal process. Vestigial stigmata slightly darker than sterna. Flagellum lanceolate, with a distal median depression undercutting a more proximal ridge. Pedipalpal trochanter produced only slightly; tarsal-basitarsal spurs about 1/6, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of unknown proportions.

Female. Abdomen not attenuate. Flagellum composed of four articles. Lateral spermathecae somewhat longer than medians, both terminating in sclerotized bulbs of nearly equal size.

Type data.—Holotype male, 19 July 1938; allotype female, 20 July 1938, both taken on Barro Colorado Island, Panama Canal Zone (E. G. Williams) (AMNH, examined).

Comparisons.—See under *S. mumai*.

Distribution.—Known only from Barro Colorado Island, Panama Canal Zone.

Remarks.—The holotype lacks the flagellum, abdominal segment XII and most of its appendages.

Additional records.—Panama Canal Zone: Barro Colorado Island, 20-24 June 1924 (N. Banks), 1 male (MCZ); 20-21 May 1964 (Chickering), 4 females (MCZ); July 1969 (S. Lawrence, B. and T. Hlavac), 2 females (MCZ); 1943-1944 (J. Zetek), 1 male (MCZ); unknown date (K. W. Cooper), 1 female (AMNH).

BRASILIENSIS GROUP

Description.—Members of this group may be small to large in size (0.91 to 1.48 mm carapacial length). Color is brownish to greenish. Eyespots are always distinct, but may vary in shape from irregular to oval to round. Carapace has three or four pairs of dorsal and two apical setae. Abdomen is never attenuated. Males: abdominal segment XII with a very slightly to well-developed posterodorsal process, which can be round, bifid, or truncate apically; flagellum usually large and nearly globose, often with elaborate dorsal modifications. Females: flagellum usually moderate in length (0.28 mm), but may be long in large species (0.48 mm), composed of three articles; usually with two pairs of spermathecae of similar size; apical portions of spermathecae sometimes extremely large, almost circular, and highly sclerotized, whereas other individuals have considerably smaller unsclerotized bulbs. Pedipalps are usually highly dimorphic, but variably so; a slight elongation is usually manifest, but more often the segments are heavily developed; trochanter is noticeably produced; femur and patella sometimes have a mesal tooth.

Remarks.—Table 5 gives characters used in separating the species of the *brasiliensis* group.

Distribution.—México: Oaxaca, Tabasco, Chiapas. Central America: Costa Rica. South America: Colombia, Ecuador, Brazil, Bolivia.

Subordinate taxa.—*Trilobatus* complex: *S. stewarti* Rowland, *S. trilobatus* Rowland, *S. lacandonus* Rowland; *brasiliensis* complex: *S. cuenca* n. sp., *S. sturmi* (Kraus), *S. brasiliensis* (Kraus), OTU No. 7, OTU No. 8, OTU No. 9, OTU No. 10, OTU No. 11; *pallipatellatus* lineage within the *brasiliensis* complex: OTU No. 12, *S. macarensis* (Kraus), *S. cumbalensis* (Kraus), *S. pallipatellatus* n. sp.

Schizomus stewarti Rowland (Figs. 34, 35, 46)

Schizomus stewarti Rowland 1973:139-140; Rowland and Reddell 1977:80, 83, 86.

Description.—Male. Color greenish. Carapace with three pairs of dorsal and two apical setae. Eyespots distinct, irregular. Metapeltidium entire. Anterior sternum with nine bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with a slight development of posterodorsal process. Vestigial stigmata darker than sterna.

Flagellum vaguely trilobate, with a pair of slight median elevations. Pedipalpal trochanter produced acutely apically; tarsal-basitarsal spurs about $1/5$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of unknown proportions; other leg segment measurements given in Table 6.

Female unknown.

Type data.—Holotype male and paratype immature taken in Cueva del Guayabo, 12 km NE Valley Nacional, Oaxaca, México, 29 December 1972 (J. Reddell, D. McKenzie, M. McKenzie, and S. Murphy) (AMNH, examined).

Comparisons.—This species may be readily distinguished from all other species by the morphology of the pedipalp and flagellum of the male. The absence of a median depression on the flagellum serves to distinguish this species from all other members of the *brasiliensis* group.

Distribution.—Known only from the type locality.

Schizomus trilobatus Rowland
(Figs. 34, 36, 47, 62)

Schizomus trilobatus Rowland 1975b:11-13; Rowland and Reddell 1977:80, 83, 86, 99.

Description.—Male. Color greenish. Carapace with three pairs of dorsal and two apical setae. Eyespots distinct, irregular. Metapeltidium entire. Anterior sternum with 10 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with slightly rounded posterodorsal process. Vestigial stigmata darker than sterna. Flagellum strongly trilobate, with a pair of medial depressions. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about $1/5$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 42-8-6-8-7-8-15; other leg segment measurements given in Table 6.

Female. Flagellum composed of three articles. Spermathecae composed of a single pair, highly sclerotized, large, on narrow stalks.

Type data.—Holotype male and allotype female taken in Las Grutas del Coconá, Tabasco, México, 24 July 1973 (J. M. Rowland and J. R. Reddell) (AMNH, examined); paratype male and five paratype females with the same data (TTU, examined).

Comparisons.—See under *S. lacandonus*.

Distribution.—Known only from the type locality.

Remarks.—This species was collected from washed-in litter in the twilight zone of Grutas del Coconá; it shows no adaptations for a cavernicole existence. The apparent troglobite, *S. pecki* Rowland, inhabits the dark zone of this cave.

Schizomus lacandonus Rowland
(Figs. 34, 37, 48, 55, 65)

Schizomus lacandonus Rowland, 1975b:16-18.

Description.—Male. Color greenish. Carapace with three pairs of dorsal and two apical setae. Eyespots distinct, oval. Metapeltidium entire. Anterior sternum with nine bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with gently rounded, slightly developed posterodorsal process. Vestigial stigmata darker

Table 5.-Comparisons of members of the *brasiliensis* group. See the introduction to Rowland and Reddell (1979) for discussion of characters.

CHARACTER	stewarti	trilobatus	lacadonus	cuenca	sturmi	brasiliensis	OTU #7	OTU #8	OTU #9	OTU #10	OTU #11	OTU #12	macar-ensis	cumbal-ensis	pallipat-ellatus
DORSAL SETAE	3	3	3	3	3	3	3	3	3	4	3	4	3	3	3
METAPLE- TIDIUM	entire	entire	entire	split	split or entire	split	split	split	split	split	split	split	split	split	entire
STERNAL SETAE	9	10	9	11	11	11	11	11	11	11	11	11	11	11	11
PATELLA I COLOR	brown	brown	brown	brown	brown	brown	brown	brown	brown	brown	brown	white	white	white	white
COLOR	green	green	green	brown	brown	green	green	green	green	green	green	green	green	brown	green
PEDIPALP ARMATURE	none	none	none	femur	femur	femur	?	?	?	?	?	?	femur	femur	femur
ABDOMINAL PROCESS	slight	slight	slight	truncate	round	round	?	?	?	?	?	?	round	truncate	truncate
EYESPOTS	irreg- ular	irreg- ular	oval	oval	oval	irreg- ular	oval	oval	irreg- ular	irreg- ular	irreg- ular	irreg- ular	irreg- ular	oval	round
SPERMA- THECAE	?	1 pair	1 pair	?	M=L	?	M=L	M=L	M=L	M=L	M=L	M 2X L	?	M=L	M=L
CARAPACE LENGTH	1.03	1.07	1.11	1.48	1.33	1.04	.95	.91	1.09	1.33	1.02	1.08	.97	1.48	1.02
LENGTH FEM. FLAGELLUM	?	.24	.28	?	?	.25	.24	.20	.29	.38	.26	.30	?	.47	.26
PIT MALE FLAGELLUM	none	double	double	single	double	single	?	?	?	?	?	?	double	single	single

than sterna. Flagellum triangular, with a pair of median depressions. Pedipalpal trochanter produced acutely apically; tarsal-basitarsal spurs about $1/5$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 52-8-7-8-7-8-18; other leg measurements given in Table 6.

Female. Flagellum composed of three articles. Spermathecae composed of a single pair, highly sclerotized, large, on wide stalks.

Type data.—Holotype male taken at Ruinas de Palenque, Chiapas, México, 25 July 1973 (J. M. Rowland and J. R. Reddell) (AMNH, examined); allotype female taken at Ruinas de Palenque, 6 July 1949 (C. J. Goodnight) (AMNH, examined).



Fig. 34.—Map showing distribution of schizomids of the *brasiliensis* group: 1, *S. stewarti*; 2, *S. trilobatus*; 3, *S. lacandonus*; 4, *S. pallipatellatus*; 5, OTU No. 9; 6, *S. sturmi*; 7, *S. macarensis*; 8, OTU No. 8; 9, *S. brasiliensis*; 10, *S. cumbalensis*; 11, OTU No. 12; 12, OTU No. 10; 13, *S. cuenca*; 14, OTU No. 11; 15, OTU No. 7.

Table 6.—Measurements of the members of the *brasiliensis* group: 1, one male, *S. stewarti*; 2, one male, *S. trilobatus*; 3, one female, *S. trilobatus*; 4, one male, *S. lacandonus*; 5, one female, *S. lacandonus*; 6, one male, *S. cuenca*; 7, one male, *S. sturmi*; 8, one female, *S. sturmi*; 9, one male, *S. brasiliensis*; 10, one female, *S. brasiliensis*. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6	7	8	9	10
Carapace	1.03	1.09	1.07	1.18	1.16	1.48	1.35	1.33	0.95	1.04
Flagellum										
Length	0.37	0.39	0.24	0.44	0.28	0.57	0.53	-	0.38	0.25
Width	0.27	0.40	-	0.31	-	0.54	0.47	-	0.36	-
Leg I										
Femur	-	1.50	1.03	1.73	0.82	1.60	1.55	1.35	0.93	0.85
Patella	-	2.02	1.26	2.31	1.12	1.93	1.90	1.50	1.15	1.00
Tibia	-	1.52	0.91	1.81	1.51	1.39	1.35	1.15	0.80	0.73
Tarsus-basitarsus	-	0.91	0.71	1.08	1.19	1.16	1.10	0.98	0.73	0.68
Leg II										
Femur	0.61	0.83	0.68	0.90	0.80	1.14	1.03	0.93	0.62	0.60
Patella	0.34	0.45	0.41	0.50	0.43	0.61	0.55	0.45	0.35	0.25
Tibia	0.44	0.55	0.42	0.64	0.48	0.68	0.60	0.53	0.35	0.27
Basitarsus	0.41	0.54	0.41	0.53	0.44	0.66	0.57	0.55	0.35	0.32
Leg III										
Femur	0.51	0.64	0.62	0.76	0.68	0.95	0.88	0.85	0.55	0.55
Patella	0.25	0.26	0.30	0.36	0.31	0.48	0.40	0.35	0.25	0.32
Tibia	0.31	0.37	0.31	0.45	0.33	0.50	0.47	0.43	0.30	0.33
Basitarsus	0.40	0.48	0.40	0.55	0.46	0.67	0.62	0.53	0.38	0.35
Leg IV										
Femur	0.98	1.29	1.02	1.49	1.16	1.54	1.43	1.30	0.95	0.90
Patella	0.33	0.55	0.48	0.62	0.49	0.76	0.62	0.55	0.46	0.40
Tibia	0.71	0.91	0.70	1.07	0.80	1.00	0.93	0.80	0.57	0.57
Basitarsus	0.55	0.79	0.61	0.89	0.69	0.96	0.85	0.78	0.50	0.50

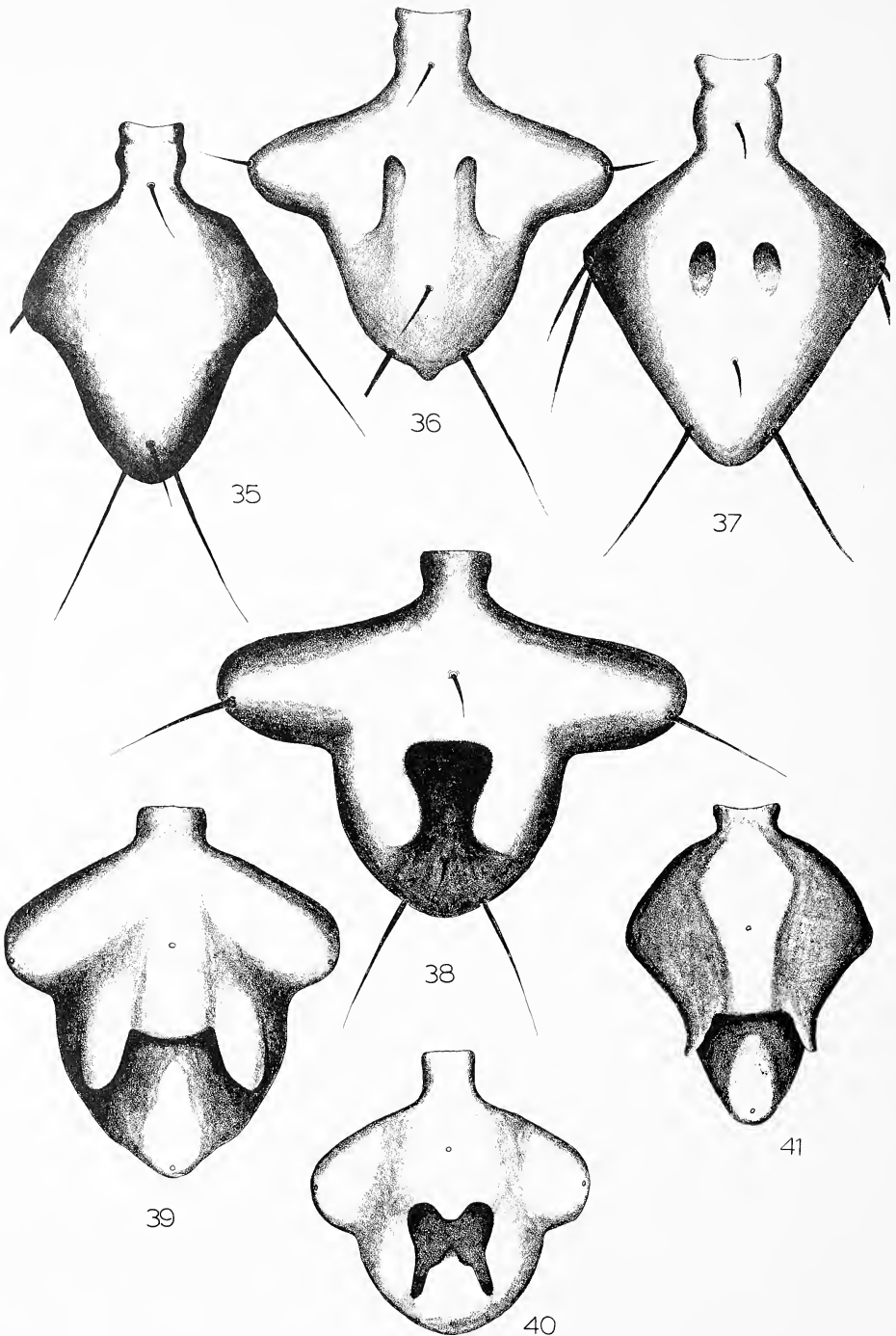
Comparisons.—This species is most closely related to *S. trilobatus*. It may most easily be distinguished from that species by the shape of the male flagellum, which is distinctly trilobate in *S. trilobatus* and triangular in *S. lacandonus*. Females of the two species are very similar but the spermathecal stalks are much wider and less strongly sclerotized in *S. lacandonus*.

Distribution.—Known only from the type locality.

Remarks.—*S. lacandonus* is one of five species known to occur in Ruinas de Palenque. Other species are *S. portoricensis* (Chamberlin), an undescribed member of the *pecki* group, an undescribed member of the *mexicanus* group, and an unplaced species. These species are all readily distinguishable on the basis of male anatomy and by external female characters and spermathecae. The unplaced species is also unique in possessing multiple setae on the abdominal terga.

Schizomus cuenca, new species
(Figs. 34, 40, 50, 53, 58)

Description.—Male. Color brownish. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Eyespots oval, distinct. Anterior sternum with 10 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with well-developed, truncate posterodorsal process. Vestigial stigmata darker than sterna.



Figs. 35-41.—Dorsal views of male flagella of the *brasiliensis* group: 35, *S. stewarti*; 36, *S. trilobatus*; 37, *S. lacandonus*; 38, *S. pallipatellatus*; 39, *S. brasiliensis*; 40, *S. cuenca*; 41, *S. cumbalensis*.

Flagellum trilobate, with a deep median depression, deeply sculptured. Pedipalpal trochanter produced acutely apically; femur with a spur; patella curved; tarsal-basitarsal spurs about 1/6, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 49-6-11-10-10-11-19; other leg segment measurements given in Table 6.

Female unknown.

Type data.—Holotype male taken in Cuenca, Ecuador, 3 April 1942 (D. and H. Frizzell) (AMNH).

Comparisons.—*S. cuenca* is most similar in the morphology of the male flagellum to *S. sturmi*, *S. pallipatellatus*, and *S. brasiliensis* in that they are all trilobate, with large lateral lobes and deep dorsal depressions. *S. sturmi* and *S. brasiliensis*, however, have two dorsal depressions, whereas *S. cuenca* and *S. pallipatellatus* have only one. The posterodorsal abdominal process of *S. pallipatellatus* is bifid, whereas in *S. cuenca* it is broadly truncate, and in *S. sturmi* and *S. brasiliensis* it is gently rounded.

Distribution.—Known only from the type locality.

Etymology.—The specific name is a noun used in apposition.

Schizomus sturmi (Kraus)
(Figs. 34, 42, 52, 56, 59, 68)

Trithyreus sturmi Kraus 1957:245, 247-249; Sturm 1958:142-143; Kraus and Beck 1967:404-405; Rowland 1972:70; Sturm 1973:113-140.

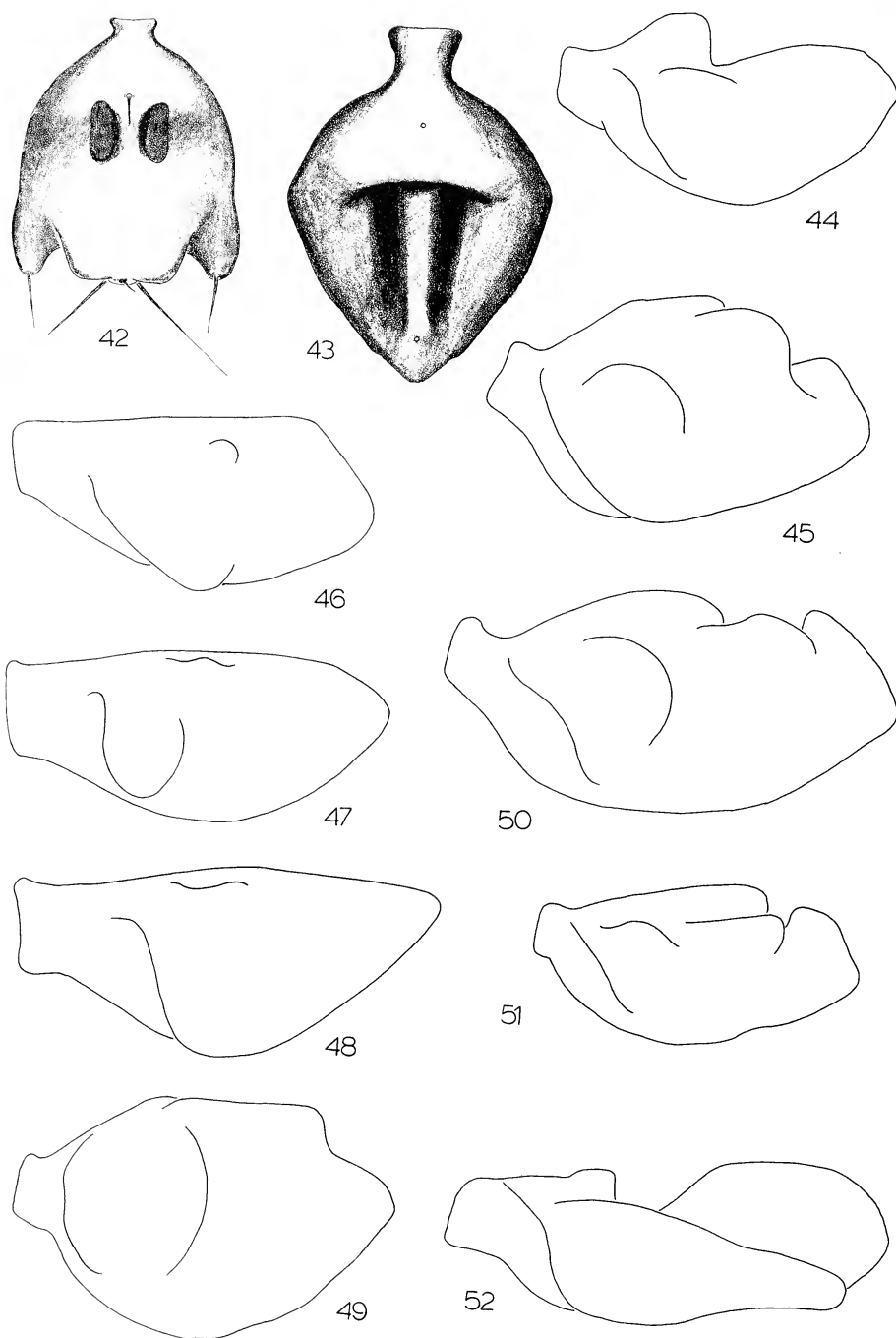
Schizomus sturmi: Rowland and Reddell 1979:

Description.—Male. Color brownish. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split or entire. Eyespots oval, distinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with gently rounded, distinct posterodorsal process. Vestigial stigmata darker than sterna. Flagellum semicircular, apically trilobate to truncate, with a pair of median depressions. Pedipalpal trochanter produced apically; femur with a spur; tibia curved; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 46-6-9-9-12-11-18; other leg segment measurements given in Table 6.

Female. Flagellum composed of three articles. Median and lateral spermathecae similar, narrow basally, expanded to nearly circular apically, with no concentration of sclerotization.

Type data.—Holotype male taken "Kolumbien: Hang am Ostrand der Hochebene von Bogota, etwa 3 km vom Stadtrand entfernt, 2800-3000 m", November 1955, April, September or October 1956 (H. Sturm) (SMF #9818, examined); six female and eight immature paratypes (SMF #9819-9821, not examined), one male paratype (AMNH, examined), and two male, two female, and one immature paratype (H. Sturm's collection, not examined), all taken with the holotype; one male, four female, and one immature paratype (SMF #9822, not examined), and one female paratype (AMNH, examined), taken "Nahere Umgebung der Stadt, 2900 m".

Comparisons.—See under *S. cuenca* for comparisons of males. The female spermathecae of *S. sturmi* are more expanded than in most species of the *brasiliensis* group, but much less so than in *S. trilobatus* and *S. lacandonus*.



Figs. 42-52.—Male flagella of the *brasiliensis* group: 42-43, dorsal views: 42, *S. sturmi*; 43, *S. macarensis*; 44-52, lateral views: 44, *S. macarensis*; 45, *S. brasiliensis*; 46, *S. stewarti*; 47, *S. trilobatus*; 48, *S. lacandonus*; 49, *S. pallipatellatus*; 50, *S. cuenca*; 51, *S. cumbalensis*; 52, *S. sturmi*.

Distribution.—Known only from near Bogota, Colombia.

Remarks.—Sturm (1958, 1973) contributed significantly to our knowledge of the behavior of schizomids through his studies of this species.

Schizomus brasiliensis (Kraus)
(Figs. 34, 39, 45)

Trithyreus brasiliensis Kraus (in Kraus and Beck) 1967:401-404; Beck 1968a:248-249; Beck 1968b:76-78; Rowland 1972:70; Brignoli 1973:3.

Schizomus brasiliensis: Rowland and Reddell 1979:

Description.—Male. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Eyespots irregular, but distinct. Metapeltidium split. Anterior sternum with 11 entire setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with gently rounded, distinct posterodorsal process. Vestigial stigmata slightly darker than sterna. Flagellum trilobate, with a deep median pit, median and lateral swellings, deeply sculptured. Pedipalpal trochanter extremely and acutely produced; femur with a spur; patella curved; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segment of leg I of unknown proportions; other leg segment measurements given in Table 6.

Female. Flagellum composed of three articles. Pedipalps unarmed. Spermathecae not studied.

Type data.—Holotype male taken "Brasilien (Amazonas): bei Manaus, Reserva Ducke des I.N.P.A., Bachsenke oberhalb des Accompanimento, Urwald mit dichtem Unterholz aus Palmen," January or February 1966 (L. Beck) SMF #11919, examined); two female and two immature paratypes taken with the holotype (SMF #12467, 12468, examined).

Comparisons.—See under *S. cuenca*.

Distribution.—Known only from the type locality.

Remarks.—Beck (1968a, 1968b) reported on the distribution and behavior of this species.

Schizomus sp., OTU No. 7
(Figs. 34, 70)

Description.—Female. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata lighter than sterna. Flagellum composed of three articles. Pedipalpal trochanter produced slightly; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 27-4-4-5-6-5-14. Other leg segment measurements given in Table 7.

Male unknown.

Specimens examined.—Three females and four immatures taken 7 km N Leticia, Amazonas District, Brazil, 20-25 February 1972 (S. Peck) (AMNH).

Comparisons.—This species is distinct from other members of the *brasiliensis* group in that the base of the median spermathecae is much wider than the apex.

Distribution.—Known only from near Leticia, Amazonas District, Brazil.

Table 7.—Measurements of the members of the *brasiliensis* group: 1, one female, OTU No. 7; 2, one female, OTU No. 8; 3, one female, OTU No. 9; 4, one female, OTU No. 10; 5, one female, OTU No. 11; 6, one female, OTU No. 12; 7, one male, *S. macarensis*; 8, one male, *S. cumbalensis*; 9, one female, *S. cumbalensis*; 10, one male, *S. pallipatellatus*; 11, one female, *S. pallipatellatus*. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6	7	8	9	10	11
Carapace	0.95	0.91	1.09	1.33	1.02	1.08	0.97	1.50	1.48	0.94	1.02
Flagellum											
Length	0.24	0.20	0.29	0.38	0.26	0.30	0.35	0.66	0.47	0.38	0.26
Width	-	-	-	-	-	-	0.28	0.50	-	0.49	-
Leg I											
Femur	0.76	0.80	1.04	1.23	0.91	1.07	1.05	1.55	1.35	0.97	0.91
Patella	0.88	0.93	1.12	1.45	1.03	1.26	1.28	1.83	1.60	1.15	1.04
Tibia	0.62	0.65	0.85	1.08	0.72	0.92	0.95	1.38	1.18	0.82	0.76
Tarsus-basitarsus	0.65	0.60	0.78	0.88	0.65	0.77	0.80	1.20	1.02	0.69	0.66
Leg II											
Femur	0.52	0.58	0.74	0.90	0.68	0.74	0.70	1.20	1.07	0.63	0.66
Patella	0.31	0.30	0.40	0.49	0.38	0.42	0.37	0.62	0.60	0.28	0.33
Tibia	0.32	0.32	0.41	0.53	0.40	0.44	0.40	0.72	0.62	0.38	0.38
Basitarsus	0.32	0.33	0.40	0.50	0.39	0.44	0.43	0.70	0.60	0.35	0.35
Leg III											
Femur	0.51	0.50	0.62	0.79	0.59	0.65	0.60	1.05	0.95	0.54	0.57
Patella	0.24	0.25	0.29	0.41	0.29	0.31	0.36	0.50	0.47	0.25	0.25
Tibia	0.24	0.25	0.33	0.40	0.31	0.32	0.30	0.57	0.50	0.28	0.30
Basitarsus	0.33	0.33	0.40	0.56	0.41	0.45	0.43	0.72	0.62	0.37	0.35
Leg IV											
Femur	0.87	0.90	1.05	1.26	0.93	1.07	1.05	1.58	1.45	0.91	0.93
Patella	0.36	0.35	0.48	0.61	0.41	0.47	0.40	0.70	0.68	0.38	0.41
Tibia	0.52	0.55	0.68	0.84	0.63	0.71	0.62	1.05	0.93	0.60	0.59
Basitarsus	0.51	0.47	0.63	0.81	0.58	0.66	0.57	0.98	0.87	0.53	0.56

Schizomus sp., OTU No. 8
(Figs. 34, 61)

Description.—Female. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Eyespots oval, distinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata lighter than sterna. Flagellum composed of three sections. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 24-4-4-4-5-6-13; other leg segment measurements given in Table 7. Both median and lateral spermathecae very similar in form and shape; slightly divergent, not expanded distally; unevenly sclerotized along most of the length.

Male unknown.

Specimen examined.—Female taken at Santarem, Taperinha, Brazil, 29 October 1970 (S. L. Tuxen) (UZMK).

Comparisons.—This species is very similar in spermathecal morphology to OTU Nos. 9-11, but is distinct in having the spermathecae very narrow.

Distribution.—Known only from Santarem, Taperinha, Brazil.

Schizomus sp., OTU No. 9
(Figs. 34, 69)

Description.—Female. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Eyespots distinct, irregular. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata lighter than sterna. Flagellum composed of three articles. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about $1/4$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 34-4-6-6-7-7-14; other leg segment measurements given in Table 7. Both median and lateral spermathecae of about equal size; medians terminate in bulbs about twice diameter of those of laterals; both sclerotized; stalk of laterals about twice as wide as that of medians, expanded basally.

Male unknown.

Specimen examined.—Female taken at El Saladito, Valle, Colombia, 29 August 1967 (P. Wygodzinsky) (AMNH).

Comparisons.—This taxon appears to be most closely related to OTU No. 12 in having the spermathecal walls slightly thickened apically. The terminal bulbs are more distinct in OTU No. 9 than in OTU No. 12.

Distribution.—Known only from El Saladito, Valle, Colombia.

Schizomus sp., OTU No. 10
(Figs. 34, 63)

Description.—Female. Color brownish green. Carapace with four pairs of dorsal and two apical setae. Metapeltidium split. Eyespots irregular, distinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum composed of three articles. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about $1/5$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 39-4-7-7-8-8-15; other leg segment measurements given in Table 7. Median and lateral spermathecae small, similar, slightly smaller apically in the laterals, but both expanded distally into small circular to oval terminal bulbs.

Male unknown.

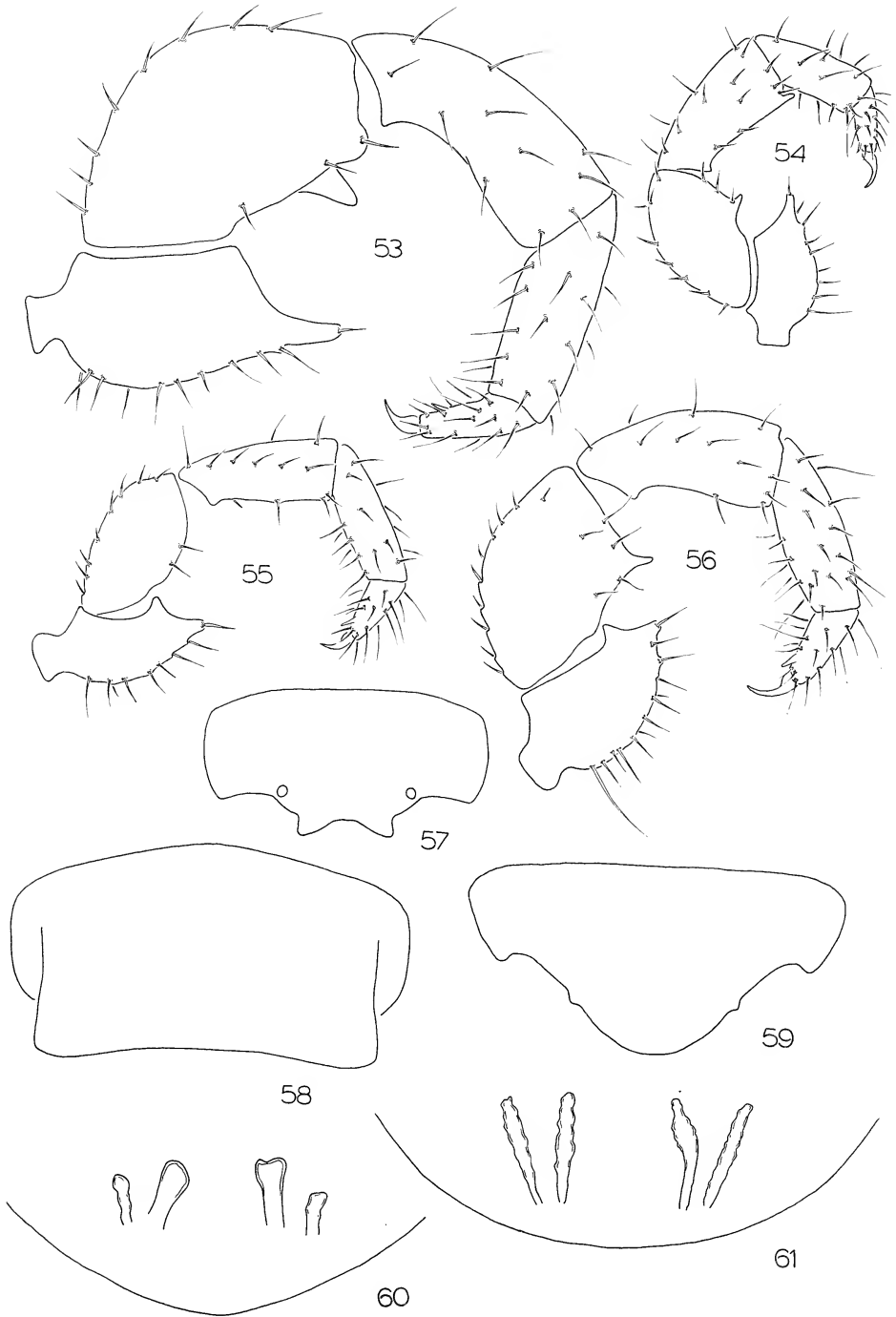
Specimens examined.—Female and immature taken at “Dolline de la grotte de Baños,” Baños, Ecuador, April 1965 (J. and N. Leleup) (ISB).

Comparisons.—This taxon is very similar to OTU No. 11 in the development of the spermathecae, but the terminal bulb is somewhat more distinct in OTU No. 10. OTU No. 10 is a much larger species and has a disproportionately longer flagellum than OTU No. 11.

Distribution.—Known only from Baños, Ecuador.

Schizomus sp., OTU No. 11
(Figs. 34, 64)

Description.—Female. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Eyespots irregular, distinct. Anterior sternum with 11 entire setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae.



Figs. 53-61.—Parts of schizomids of the *brasiliensis* group: 53-56, lateral views of male right pedipalps: 53, *S. cuenca*; 54, *S. pallipatellatus*; 55, *S. lacandonus*; 56, *S. sturmi*; 57-59, dorsal views of male posterodorsal abdominal process: 57, *S. pallipatellatus*; 58, *S. cuenca*; 59, *S. sturmi*; 60-61, female spermathecae: 60, OTU No. 12; 61, OTU No. 8.

Vestigial stigmata lighter than sterna. Flagellum composed of three articles. Pedipalpal trochanter produced slightly apically; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 26-4-5-5-6-14; other leg segment measurements given in Table 7. Median and lateral spermathecae very similar in shape and size, each gradually expanded distally, with no special sclerotization; medians convergent, laterals divergent.

Male unknown.

Specimen examined.—Female taken at Río Benicito, Chacoba, Bolivia, date unknown (W. J. Gertsch) (AMNH).

Comparisons.—See under *Schizomus* sp., OTU No. 10.

Distribution.—Known only from Río Benicito, Chacoba, Bolivia.

Schizomus sp., OTU No. 12

(Figs. 34, 60)

Description.—Female. Color brownish green. Carapace with four pairs of dorsal and two apical setae. Metapeltidium split. Eyespots distinct, irregular. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata lighter than sterna. Flagellum composed of three articles. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 31-5-6-5-8-7-15; distal half of patella white; other leg segment measurements given in Table 7. Median spermathecae about twice as long as laterals, medians slightly convergent, terminating in a sclerotized bulb, laterals lightly sclerotized along distal half, terminating in a slight bulb.

Male unknown.

Specimen examined.—Female taken at Oriente Río Negro, Ecuador, April 1965 (J. and N. Leleup) (ISB).

Comparisons.—See under *S. pallipatellatus*.

Distribution.—Known only from Oriente Río Negro, Ecuador.

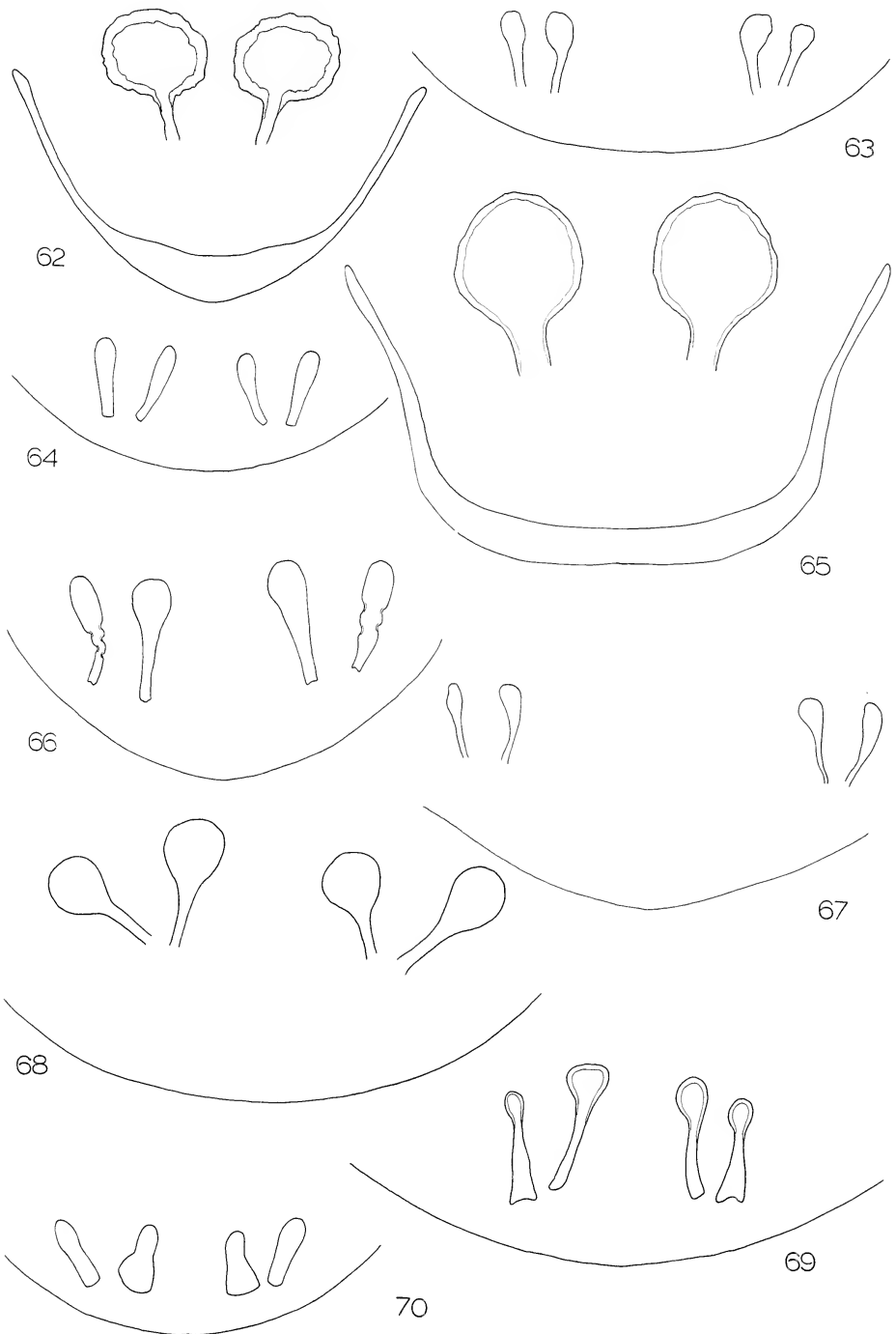
Schizomus macarensis (Kraus)

(Figs. 34, 43-44)

Trithyreus macarensis Kraus 1957:245, 249-250.

Schizomus macarensis: Rowland and Reddell 1979:

Description.—Male. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Eyespots distinct, but irregular. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with gently rounded, but distinct posterodorsal process. Vestigial stigmata darker than sterna. Flagellum oval, with a pair of median depressions, united mesally, preceded by a distinct ridge. Pedipalpal trochanter distinctly and acutely produced distally; femur with a spur; tibia curved; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 33-5-5-5-7-7-18; distal half of patella white; other leg segment measurements given in Table 7.



Figs. 62-70.—Female spermathecae of the *brasiliensis* group: 62, *S. trilobatus*; 63, OTU No. 10; 64, OTU No. 11; 65, *S. lacandonus*; 66, *S. pallipatellatus*; 67, *S. cumbalensis*; 68, *S. sturmi*; 69, OTU No. 9; 70, OTU No. 7.

Female unknown.

Type data.—Holotype male and paratype immature taken “Kolumbien: Macarena, Gebirgsstock am Fusse der Ostanden s. Villavicencio, nahe der Mündung des Rio Zanza in den Rio Guejar, 400-500 m, in der Laubstreu eines primären Hochwaldes,” 5 March 1956 (H. Sturm) (SMF #9823 and 9824, respectively, examined).

Comparisons.—See under *S. pallipatellatus*.

Distribution.—Known only from the type locality.

Schizomus cumbalensis (Kraus)

(Figs. 34, 41, 51, 67)

Trithyreus cumbalensis Kraus 1957:245, 246-247; Kraus and Beck 1967:402.

Schizomus cumbalensis: Rowland and Reddell 1979:

Description.—Male. Color brownish. Carapace with three pairs of dorsal and two apical setae. Metapeltidium split. Eyespots distinct, oval. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with squarely blunt, well-developed posterodorsal process. Vestigial stigmata darker than sterna. Flagellum triangular, deeply sculptured apically. Pedipalpal trochanter extremely produced apically; femur with spur; tibia curved; tarsal-basitarsal spurs about 1/6, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 54-7-9-10-11-11-20; distal half of patella white; other leg segment measurements given in Table 7.

Female. Flagellum composed of three articles. Median and lateral spermathecae very small, weakly developed, slightly distally expanded and equal in size.

Type data.—Holotype male taken “Süd-kolumbien: Umgebung des Ortes Cumbal, zwischen Paso und Ipiales, 3100 m,” 30 June or 5 July 1956 (H. Sturm) (SMF #9816, examined); two female and four immature paratypes (SMF #9817, examined), and one female and two immature paratypes (H. Sturm's collection, not examined), taken with the holotype.

Comparisons.—See under *S. pallipatellatus*.

Distribution.—Known only from the type locality.

Schizomus pallipatellatus, new species

(Figs. 34, 38, 49, 54, 57, 66)

Description.—Male. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Metapeltidium entire. Eyespots distinct, round. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae; segment XII with well-developed, truncate posterodorsal process with a pair of lateral projections. Vestigial stigmata lighter than sterna. Flagellum trilobate, with a median depression flanked by a pair of whitish processes. Pedipalpal trochanter produced acutely apically; femur and patella with spurs; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 27-6-5-5-6-6-14; distal half of patella white; other leg segment measurements given in Table 7.

Female. Flagellum composed of three articles. Median and lateral spermathecae distally expanded gradually, the laterals with subdistal constrictions, no areas of concentrated sclerotization.

Type data.—Holotype male, 23 October 1957, allotype female and immature paratype, 12 September 1957, paratype female, 26 October 1957, paratype immature, 25 June 1957, immature paratype, 19 June 1957, female and two immature paratypes, 19 July 1957, all taken at Coto, Costa Rica (E. Dixon); female and immature paratypes taken at Golfito, Costa Rica, 17 September 1957 (E. Dixon). All specimens deposited in the AMNH.

Comparisons.—*S. pallipatellatus* shares with OTU No. 12, *S. macarensis*, and *S. cumbalensis* a white patella I. This character alone separates these four species from all other members of the *brasiliensis* group. Females of *S. pallipatellatus* have much more greatly expanded spermathecae than do those of OTU No. 12. The spermathecae of *S. pallipatellatus* are much larger than are those of *S. cumbalensis*. The shape of the male flagellum readily serves to distinguish *S. pallipatellatus* from *S. cumbalensis* and *S. macarensis*, being distinctly trilobate in *S. pallipatellatus*, while more apically attenuate in *S. cumbalensis* and nearly oval in *S. macarensis*.

Distribution.—Known from Coto and Golfito, Costa Rica.

Etymology.—The specific name is taken from the Latin *palli*-meaning lacking in color and *patella* referring to the distinctive white coloration of the patella of the first pair of legs.

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COURTSHIP BEHAVIOR, HABITAT, AND REPRODUCTIVE ISOLATION IN *SCHIZOCOSA ROVNNERI* UETZ AND DONDALE (ARANEAE: LYCOSIDAE)

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ABSTRACT

The courtship behavior of *Schizocosa rovnneri* Uetz and Dondale is described and analyzed. Courtship behavior in this species is distinct from that of *Schizocosa ocreata* (Hentz), although these species are morphologically very similar and indistinguishable on the basis of genitalia.

Males of both species courted conspecific and heterospecific females with almost equal frequency. However, females only responded receptively and copulated with conspecific males. Males of *S. rovnneri* exhibited quantitative differences in aspects of courtship behavior in response to different stimuli. In the presence of a conspecific female, the searching phase was shorter and less variable, and the stridulation bouts were three times as frequent than with heterospecific females. Values of these parameters for male *S. rovnneri* with only the silk (and pheromone) of a conspecific female were intermediate.

Data on habitat and seasonal occurrence of the two species suggest that *S. ocreata* breeds earlier in the season and prefers upland forest areas, while *S. rovnneri* breeds 2-3 weeks later and prefers bottomland forest and river flood plains. It is suggested that differences in courtship behavior serve to maintain reproductive isolation in these two species, whose spatial and temporal isolation is incomplete.

INTRODUCTION

A wide variety of animals have been studied with respect to reproductive behavior, and it is suggested that in many the sequences of behaviors leading to copulation functions to ensure reproductive isolation (Crane 1955; Jacobs 1955; Stride 1956, 1958). Hybrids between populations are frequently less fit than either parent. When this occurs, selection acts to prevent reproductive "mistakes" (Bush 1975). Individuals possessing characteristics which emphasize differences between populations (courtship and mating factors) will contribute more offspring to future generations (White 1978).

It is possible that a variety of arthropod populations that rarely interbreed in nature are capable of doing so, but owing to seasonal and habitat differences, and possibly reproductive behavior, do not actually interbreed. A species reproductively isolated from other groups by behavioral mechanisms occurring in courtship is known as an "etho-species" (Hollander and Dijkstra 1974). This definition becomes useful when morphological characteristics are indistinct between groups or show a large gradation (Hollander et al. 1973).

Arthropod systematists have traditionally relied heavily on morphological characteristics of genitalia in determining species, but are the first to admit to the limitations of the method. The logic behind the system is sound enough - morphological differences in genitalia serve to maintain reproductive isolation in a "lock-and-key" fashion (Gering 1953). This line of reasoning cannot explain cases of identical genitalia that do not interbreed. These species are known as "cryptic" species, as they often go undetected (Walker 1964). Studies of calling songs and reproductive communication in crickets and longhorned grasshoppers have revealed numerous species that were unrecognized on the basis of morphological studies (Walker 1957). It is estimated that a sizeable number of species in a variety of animal taxa are cryptic by commonly used taxonomic standards, yet are reproductively isolated and thus are valid species just the same.

Clarification of taxonomic problems with interbreeding experiments and behavioral studies has been attempted with spiders with a high degree of success (Taylor and Peck 1975; Dondale 1964, 1967; Rovner 1973). Hollander et al. (1973) examined reproductive barriers in *Pardosa* (Araneae: Lycosidae), and found habitat, seasonality and courtship behavior to be of great importance in clarifying species relationships. Hollander and Dijkstra (1974) discovered an ethospecies, *Pardosa vlijmi*, separated from a sibling species by courtship behavior alone.

This paper concerns behavioral clarification of species identity in the recently revised North American spider genus *Schizocosa* (Araneae: Lycosidae) (Dondale and Redner 1978). *Schizocosa ocreata* (Hentz) is a wolf spider common in deciduous forest litter in eastern North America. *Schizocosa rovneri*, Uetz and Dondale, from Illinois is apparently identical to *S. ocreata* with respect to genital characters, body size, general morphology, color, etc. It does, however, lack the prominent (although variable) tufts of black bristles on the tibiae of leg I present on males of *S. ocreata*. The courtship and mating behavior of these two species is clearly different; and females will copulate only with conspecific males. It is probable that *S. rovneri* is a valid ethospecies, reproductively isolated from *S. ocreata* by courtship behavior.

METHODS

During the course of doctoral research at the University of Illinois (1972-1976), one of us (GU) collected large numbers of specimens of *Schizocosa* wolf spiders. These specimens were identified as *S. ocreata* (at that time called *S. crassipes*) on examination of genital characters. However, males lacked the characteristic tufts of dense black bristles on the tibia of leg I. Similar specimens had been reported in Delaware (Uetz 1977), in Arkansas (Peck and Whitcomb, in press), and North Carolina (Berry 1971). Our original intent was to determine if internal parasites were suppressing development of the tibial brushes in individuals from Illinois. The brushes are a secondary sexual characteristic and would be likely to be lacking in cases of parasitic castration. Finding no parasites, we attempted to crossmate individuals from brushless and typical populations to see if they were reproductively compatible.

Individuals of the suspected new species, *S. rovneri*, were collected as immatures in the antepenultimate instar in March 1977, in the flood plain of Hart Memorial Woods, located on the Sangamon River near Mahomet, Illinois. Field data on phenology and habitat were available from a pitfall trap study on the Sangamon River nearby (Uetz 1976). In May 1977, immature *S. ocreata* in the penultimate instar were collected at Strouds Run State Forest near Athens, Ohio. Specimens were housed separately in in-

Table 1.—Behavioral responses of male and female *Schizocosa* to the presence of other individuals or their silk (and pheromones). (+) indicates a positive response (courtship if the specimen is a male; receptivity if the specimen is a female), while (–) indicates no response or a negative response (avoidance or agonistic behavior).

	<i>S. ocreata</i> (Ohio)		<i>S. rovneri</i> (Illinois)	
	+	–	+	–
MALES				
with conspecific female	8	1	11	1
with conspecific female silk (and pheromone)	10	0	10	0
with heterospecific female	9	1	8	0
with heterospecific female silk (and pheromone)	10	0	10	0
FEMALES				
with conspecific male	6	3	11	1
with heterospecific male	0	8	0	10

dividual, clear plastic, rectangular containers (7cm x 7cm x 13cm). Each container had a cotton-plugged vial filled with water, which provided a source of moisture. Each spider was fed a mealworm (*Tenebrio molitor* L.) every 3-5 days. All spiders were placed in a growth chamber in order to insure a natural day/night temperature and light cycle (23°C day, 13°C night; with 13 hours light; 11 hours dark) and prolong the life of the specimens.

Mating experiments for this study took place in late May and early June 1977. Tests were conducted in a circular culture dish (19cm diam; 7cm depth) with a piece of white bond paper covering the floor of the container. Females of either species were placed in the container and allowed to move freely for 3-5 hours. They were removed and a conspecific or heterospecific male was placed in the container and observed for 20 min. for evidence of courtship response to the silk and/or pheromone present in the silk. Courtship behavior of males with a female present was observed by placing a plastic divider in the culture dish, separating the male and female. Conspecific and heterospecific pairs were observed for twenty minutes, and evidence of female receptivity was noted. Courtship behavior was recorded on film and descriptive accounts of the behavior were whispered into a tape recorder while observing the specimens. A stop watch was used to record the time intervals between stridulation and the time of searching behavior. In some cases individuals were allowed to come in contact with each other (without the divider).

RESULTS

Courtship behavior was displayed by males of *Schizocosa rovneri* and *S. ocreata* in most test cases (Table 1). Males of both groups courted conspecific and heterospecific females with almost equal frequency. However, females only responded receptively in the presence of a conspecific male.

The behavior of receptive female *S. rovneri* closely resembled that of *S. saltatrix* (Rovner 1974). The female lowered her cephalothorax and extended her forelegs on the substrate, then rose, turned 90°-180° in the opposite direction and repeated the procedure. Several turns were executed in rapid succession, followed by mounting by the male

Table 2.—Comparison of courtship behavior of *Schizocosa* males.

Behavioral Phase	<i>S. ocreata</i> (Ohio)	<i>S. rovneri</i> (Illinois)
Searching	distinct in-unison raising of first pair of legs, tapping on substrate; palpal movements—stridulation	legs extended, probing in random fashion, palpal movements without stridulation (palps scraped on substrate, then alternately raised and moved past chelicerae)
Display	forelegs alternately raised, arched, and extended forward	forelegs extended in contact with substrate; spine erection over entire body; body raised, then lowered rapidly and bounced on substrate; impact of bounce produces abdominal reverberations
Stridulation	barely audible; accompanies leg tapping	audible; producing a “buzzing” sound; occurs in short bursts accompanying “bounce”

(when the divider was removed). Female *S. rovneri* exhibited this sequence of behaviors in the presence of conspecific males in 11 out of 12 trials, but never in the presence of heterospecific males.

Several conspecific matings were allowed for each group by removing the divider. Copulation was characteristic for the genus, as described by Rovner (1973), and resulted in offspring in all cases. Heterospecific pairings without the divider never resulted in copulation despite numerous attempts by males to mount. Females in these cases responded to males with avoidance or agonistic behavior.

The courtship behavior of *Schizocosa rovneri* differed in many respects from that of *S. ocreata* (Table 2). The courtship sequence began with a searching phase, which consisted of raising, extending and lowering the forelegs in a probing fashion. A series of rapid palpal scraping movements occurred during searching, followed by alternately raising the palps to the chelicerae. Tietjen (pers. comm.) has suggested that these behaviors are associated with the cleaning of silk from pedipalps and not with olfaction. After a variable number of palpal scraping movements, the male entered a stationary phase wherein the legs were extended and the palps were held perpendicular to and in contact with the substrate. The display phase which followed consisted of several bouts of stridulation (produced by the stridulatory organs in the male palp (Rovner 1975), which produced a clearly audible sound characterized as a “buzz”. This was followed by a brief period of inactivity, after which the spider would either go through another entire courtship sequence beginning at the searching phase, or change position and resume stridulation.

Analysis of high speed films (58 fps) of courtship in *S. rovneri* males has revealed a unique movement of the entire body associated with stridulation. The spider first raised the cephalothorax and abdomen slightly, then thrust the body downward between the legs, hitting the substrate with a “bounce”. Rotating movements of the palps were observed at this point, indicating stridulation. Reverberation of the bounce impact was noted in the entire body, and was particularly visible in the abdomen, which continued to vibrate for a few fractions of a second. The onset of stridulation and reverberation of the

Table 3.—Quantitative analysis (means indicated with ± 1 S.E.) of behavior exhibited by *S. rovneri* males during courtship. (*=only two measurements available; **=means are significantly different [T-test; $p<0.01$]).

	N	No. exhibiting courtship	\bar{x} time in searching mode (sec)	\bar{x} stridulation frequency (no./10 sec)	\bar{x} interval between bouts of stridulation**
with conspecific female	10	9	30.44 \pm 2.89	2.06 \pm .17	12.23 \pm 3.28
with conspecific silk (and pheromone)	10	10	61.80 \pm 19.26	2.39 \pm .35	28.04 \pm 4.53
with heterospecific female	5	5	48.20 \pm 11.05	1.65 \pm .35	35.0 \pm 85.0*
with heterospecific silk (and pheromone)	10	10	46.78 \pm 14.86	2.35 \pm .21	63.48 \pm 18.53

bounce impact were simultaneous and appear (when viewed at normal speed) as a “jerk” or “spasm”.

Although males of *S. rovneri* and *S. ocreata* displayed to conspecific and heterospecific females and in response to their silk, there is evidence that male *S. rovneri* exhibit quantitative differences in courtship behavior in response to different stimuli (Table 3). There was a significant decrease in the variability of searching time when males were placed with conspecific females, as compared with all other trials, although mean search time was not significantly different. The time interval between bouts of stridulation was significantly decreased ($p<0.01$) in the presence of conspecific females and their silk vs. heterospecific females or their silk. Also, interval time was significantly lower in the presence of conspecific females vs. pheromone alone ($p<0.01$).

DISCUSSION

Observations made in the laboratory of *S. ocreata* and the new species *S. rovneri* clearly indicate that there is a significant difference in courtship behavior of the two groups. This is important in light of the fact that the two groups are morphologically identical with respect to genital characteristics. The only apparent morphological difference between the groups is that male *S. ocreata* have a dense brush of black setae on the tibia of leg I which is absent in *S. rovneri*. It is possible that the brush is important in the courtship behavior of *S. ocreata*, which includes raising, extension and tapping of the first pair of legs. The brush might provide an important visual cue for the female. *S. rovneri* seems to rely less on the visual aspects of courtship; but rather, relies heavily on the auditory effect of vibrations created by the stridulatory organs on the male palp.

Behavioral differences were not only noted between *S. ocreata* and *S. rovneri* but also within the response of *S. rovneri* to conspecific and heterospecific females and their silk. Silk of adult female wolf spiders has been shown to contain a sex pheromone which elicits the courtship response of male spiders (Rovner 1968). Male *S. rovneri* displayed courtship in almost all trial cases. However, in the presence of a conspecific female, the searching phase was shorter and less variable, and the stridulation bouts more frequent. Without a plastic barrier, copulation occurred within two minutes in most cases. In cases of male *S. rovneri* with heterospecific female or silk of either species, the searching phase was longer

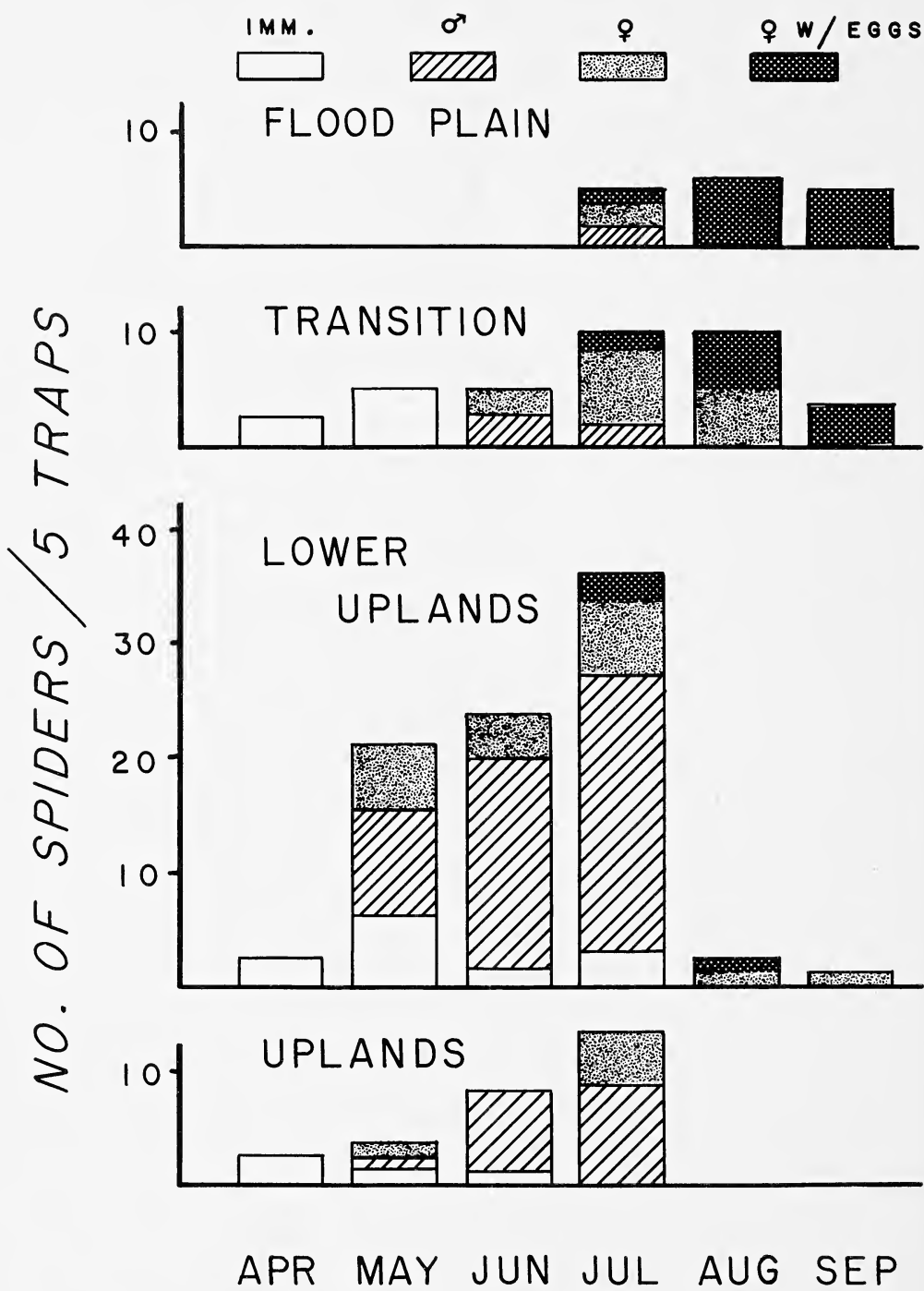


Fig. 1.—Seasonal abundance of *Schizocosa rovneri* at four elevations on a flooding gradient. The site is the streamside forest at Robert Allerton Park, on the Sangamon River in central Illinois.

and more variable and courtship was not as vigorous in terms of frequency of stridulation bouts. This suggests that the male *S. rovneri* court conspecific females more readily and more efficiently in response to some recognition factor.

It appears that the female response is ultimately the critical factor in the isolation of these two species. While males of each species court females of both species, the females only respond to and copulate with members of their own species. Female *S. rovneri* respond almost immediately to the stridulation of male *S. rovneri* but not to the palpal tapping of *S. ocreata*. It is clear that sexual communication through stridulation plays a major role in the reproductive isolation of these species.

Our collections of *Schizocosa rovneri* (as well as collections mentioned in the literature we suspect are *S. rovneri*—Berry 1971; Uetz 1977; Peck and Whitcomb, 1978) are well within the geographic range of *S. ocreata*. Interestingly, the microhabitat preferences and seasonal occurrence of all four populations of suspected *S. rovneri* were similar to each other, yet distinct from *S. ocreata* populations. *Schizocosa ocreata* is common in Illinois, and has even been taken in the same study area where we collected *S. rovneri*. Data on habitat and seasonal occurrence are available on both species, and suggest that *S. ocreata* breeds earlier in the season and prefers upland forest areas. *S. rovneri* breeds later and prefers bottomland forest habitat and river flood plains. It is a species in which habitat, seasonality and behavior interact in reproductively isolating the species from others. Pitfall trap collections of *S. rovneri* at different elevations in an Illinois flood plain forest over the breeding season show the influence of vernal flooding on the temporal and spatial occurrence of the new species (Figure 1). We might hypothesize that populations of *Schizocosa* occurring in low-lying areas have a later season of breeding than populations in higher areas, and are phenologically "out of phase" with upland populations.

Differences in courtship behavior would appear to be important in maintaining the reproductive isolation of the two groups (since they are not completely isolated by habitat or season), and thus are crucial in maintaining species' genetic integrity. For this reason, we feel *Schizocosa rovneri* is a valid "etho-species". Further research is currently underway to determine interfertility of populations, and to examine geographic variability in behavior. New information will aid our understanding of the problematical taxonomy of the Lycosidae.

ACKNOWLEDGMENT

We would like to acknowledge the assistance of several persons in unraveling the mystery of this new species. Charles Dondale examined specimens and provided encouragement through frequent correspondence. Bill Tietjen, Alan Cady, and Gail Stratton shared insights and information. Jerry Rovner gave us his time and shared the wealth of his experience with lycosid behavior. Kitty Kaupisch typed the manuscript. For all this, we are most grateful.

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NEW SPECIES OF *PELLENES* FROM CALIFORNIA (ARANEAE: SALTICIDAE)

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ABSTRACT

Five new species of jumping spiders from California are described, and named as follows: *Pellenes* (*Habronattus*) *ustulatus*, n. sp., *Pellenes* (*Habronattus*) *icenoglei*, n. sp., *Pellenes* (*Habronattus*) *kawini*, n. sp., *Pellenes* (*Habronattus*) *kubai*, n. sp., and *Pellenes* (*Habronattus*) *schlingeri*, n. sp.

INTRODUCTION

In conjunction with a study of the subgenus *Habronattus* F. P. Cambridge 1901 of the genus *Pellenes* Simon 1876 in California, five new species were discovered. I wish to thank the following for the loan of specimens: Saul Frommer, University of California, Riverside (UCR); Wendel Icenogle, personal collection (WIC); Norman Platnick, American Museum of Natural History (AMNH); Elbert L. Sleeper, California State University at Long Beach (CSULB); and Mel Thompson, personal collection (MTC). Other specimens were from the California Insect Survey, University of California, Berkeley (CIS) and the collection of the author (CEG).

The ratios given in the descriptions were calculated as follows: A — length ocular field/length carapace; B — length tibia III/tibia IV; C — height clypeus/height face; D — length ocular field/height carapace (to top of PLE); E — length patella III/tibia III; F — length tibia I/width ocular field III; G — length femur I/width ocular field III; H — length femur III/width ocular field III; I — length femur IV/femur III; J — length basitarsus and telotarsus I/tibia I; K — width ocular field III/length carapace.

Pellenes (*Habronattus*) *ustulatus*, new species
Figs. 1, 2.

Types.—Male holotype from Del Puerto Canyon, at N. Fork, Del Puerto Creek, Stanislaus Co., California, 12 April 1975, (C. E. Griswold), California Insect Survey, deposited on indefinite loan in the California Academy of Sciences. Two paratype males (same

locality): 13 April 1974 and 29 April 1975 (C. E. Griswold), in CIS. Specific name from the Latin for scorched, singed, or browned, referring to the color of the spider and the hot, dry situations in which it has been collected.

Male.—Carapace with integument dark brown, black around eyes; thin black marginal line; sides clothed with tan scales, ocular area densely covered with short scales of same color; band of black scales between PLE and ALE; patch of white scales behind each anterior eye; a few red-brown scales between each anterior eye. Clypeus with integument tan, dark line beneath each AME; tan-white scales from sides of carapace extending toward middle; long reddish-tan scales forming sparse fringe at oral margin. Chelicera brown at base, fading to pale yellow-brown at tips; few scales above. Labium and endite dusky brown, white at tips; sternum dusky brown, lightest in center; coxae and trochanters pale yellow-white. Abdomen with integument of dorsum dark anteriorly, breaking up into light and dark chevrons posteriorly; venter pale yellow-white; uniformly covered on dorsum and sides with tan scales; white scales on venter; spinnerets pale yellow. First leg with femur yellow-brown on dorsal and posterolateral surfaces, pale ventrally, and with dusky markings on anterolateral surface; sparse, fine black hairs on anterolateral surface; short, black posteroventral fringe on distal 0.25 of segment; patella, tibia, and basitarsus yellow-brown on dorsal and upper part of anterior surface, this area covered with white scales; lower part of anterior and ventral surface densely covered with black scales; telotarsus pale yellow-brown. Legs II-IV with integument yellow-brown, with dusky brown annuli basally and subapically on femora, basally and apically on patellae to basitarsi; claw tufts contrasting black. Palpus with segments yellow-brown; tarsus covered with white hairs; tibial apophysis as in fig. 2; bulb as in fig. 1.

Measurements.—Total length 3.92 mm; carapace length 2.13 mm; LOF 1.14 mm; WOF III 1.52 mm; carapace height 1.14 mm; face height 0.61 mm; clypeus height 0.19 mm; femur I length 1.1 mm; tibia I length 0.72 mm; basitarsus and telotarsus I length 1.03 mm; femur III length 1.52 mm; patella III length 0.76 mm; tibia III length 0.84 mm; femur IV length 1.10 mm; tibia IV length 0.68 mm.

Ratios.—A = 0.54, C = 0.31, D = 1.0, F = 0.475, G = 0.70, H = 1.0, I = 0.725, J = 1.42, K = 0.71.

Female.—Unknown.

Diagnosis.—*P. ustulatus* differs from other members of the genus in having the carapace and abdomen almost uniformly covered with tan scales, the first patella, tibia, and basitarsus black beneath, and in details of the palpal bulb.

Natural History.—Specimens have been collected on dry ground beneath *Adenostema fasciculatum* H. & A., and on gravelly soil; species apparently prefers hot, dry habitat.

Distribution.—Known only from type locality.

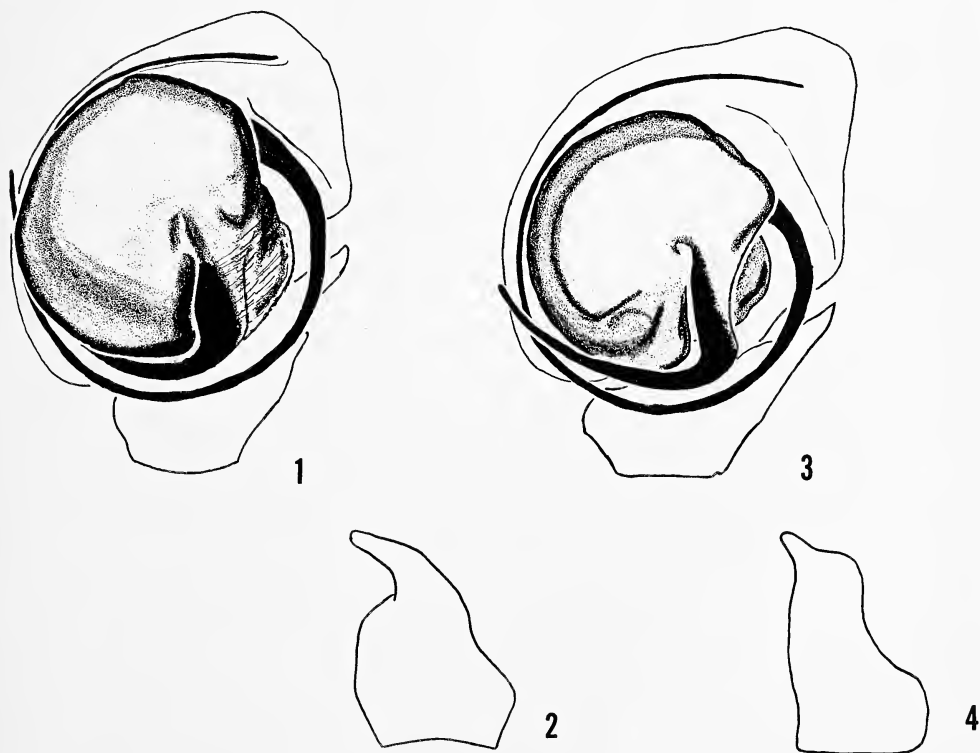
Pellenes (Habronattus) icenoglei, new species

Figs. 3, 4.

Type.—Male holotype from Indio, Riverside Co., California, 13 August 1962, (D. Gilmore), (CSULB), deposited in collection of California Academy of Sciences. The specific name is a patronym in honor of Wendel Icenogle.

Male.—Carapace with integument of ocular area dark brown; sides with broad brown band, one-half as wide as height of carapace, extending back toward posterior margin of carapace; triangular dark marking extending from ocular area down posterior declivity, widest behind; area around this marking forming yellow-brown band, extending to lower

margin and from base of triangle extending forward on lower margin of carapace to below level of PME; thin brown line around lower margin of carapace; ocular area overlain by white scales, these broadest posteriorly, becoming narrower and grayer above anterior eye row; white scales on areas of light integument and brown scales on areas of dark integument; color of integument plainly showing through on all areas; white scales around lower margin. Clypeus with integument yellow-brown centrally, becoming dusky laterally and extending on sides to below level of PME; covered with snow white scales; oral margin with fringe of long white hairs. Chelicera with integument yellow-brown, darkest above; covered with white hairs arising from upper part of chelicera and equal to chelicera in length. Labium, endite, sternum, coxae, and trochanters pale yellow-white, unmarked. Abdomen with integument pale yellow-white; dorsum with dusky marking in front, diverging into two broad longitudinal bands which reunite just before spinnerets, area between these bands white; venter unmarked; dorsum with areas of light integument covered with long white scales; dark integument covered with long brown scales. Legs with integument yellow-white, unmarked; leg I with orange scales, few distally on femur, dense on anteriodorsal and lateral surfaces of patella and tibia, and sparse on basitarsus; leg II with orange scales arranged as leg I, but much sparser; legs III and IV with scattered white scales. Palpus with all joints pale, covered with white hairs; tibial apophysis and bulb as in figs. 3, 4.



Figs. 1-2.—*Pellenes ustulatus*, new species: 1, ventral view of male palp; 2, retrolateral view of male palpal tibia.

Figs. 3-4.—*Pellenes icenoglei*, new species: 3, ventral view of male palp; 4, retrolateral view of male palpal tibia.

Measurements.—Total length 4.29 mm; carapace length 0.99 mm; face height 0.61 mm; clypeus height 0.23 mm; femur I length 1.10 mm; tibia I length 0.76 mm; basitarsus and telotarsus I length 1.14 mm; femur III length 1.44 mm; patella III length 0.80 mm; tibia III length 0.72 mm; femur IV length 1.25 mm; tibia IV length 0.80 mm.

Ratios.— $A = 0.47$, $C = 0.37$, $D = 0.96$, $F = 0.54$, $G = 0.76$, $H = 1.0$, $I = 0.87$, $J = 1.5$, $K = 0.69$.

Female.—Unknown.

Diagnosis.—*P. icenoglei* may be distinguished from other members of the genus in having the patella and tibia of the first leg covered on the anterior surface with orange scales, and in having the abdomen white dorsally, with two dark converging longitudinal bands.

Variation.—Other specimens may be darker than type, with lighter areas of integument yellow-brown, and darker areas brown to black. Some specimens have dusky markings on ventur of abdomen.

Natural History.—Joshua Tree N.M. specimens were collected in pitfall traps in Creosote Bush Scrub and mixed Juniper/Yucca habitats.

Additional Specimens Examined.—CALIFORNIA: *Riverside Co.*: Joshua Tree Natl. Mon., Pleasant Valley, 1 male, "ground trap," 24 April 1967, (S. L. Jenkins, CSULB); (same), 1 male, 25 April 1965, (E. L. Sleeper, S. L. Jenkins, CSULB).

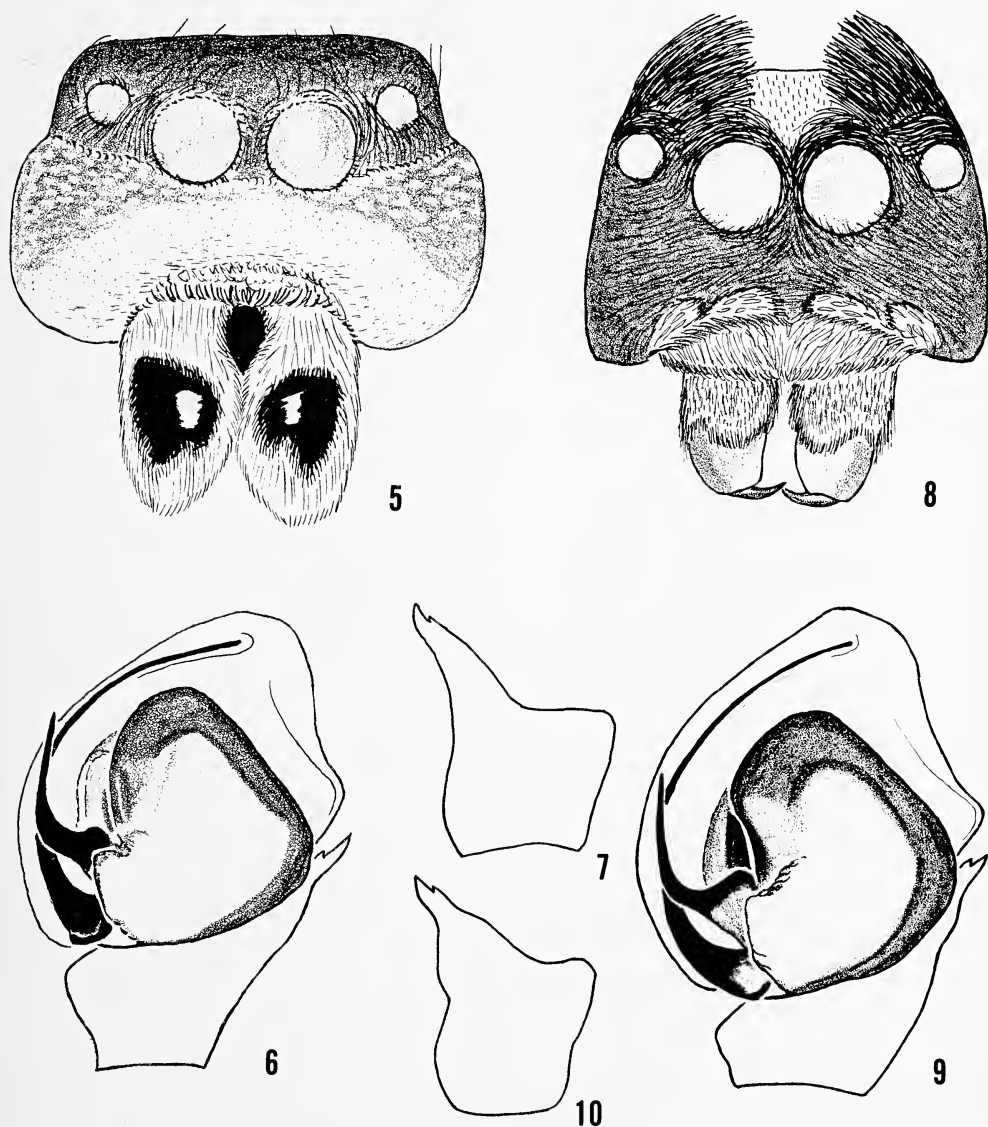
Pellenes (Habronattus) kawini, new species

Figs. 5, 6, 7.

Types.—Male holotype from Mt. Laguna, San Diego Co., California, 15 May 1975 (C. E. Griswold), California Insect Survey, deposited on indefinite loan in the California Academy of Sciences. The specific name is a patronym in honor of Richard A. Kavin.

Male.—Carapace with integument dark brown, shading to black on ocular area; ocular area densely covered with shiny dark-brown scales; cream to white scales forming faint band between PLE and ALE, sparse behind and becoming dense anteriorly; AME surrounded for upper 0.67 of their circumference by long silver blue scales; ocular area with many forward-directed, long, dark hairs, especially numerous above AME; sides with clypeal scales extending back in marginal band of diminishing width to behind level of PLE; sides and thoracic region sparsely covered with brown scales; narrow marginal band of white scales beginning at end of clypeal scales and running back to above coxa IV, and then running anterodorsally to top of declivity. Clypeus with white scales at lower margins of AME, remainder covered with closely appressed scales, extending laterally in narrowing band along lower margin of carapace to behind level of PLE; scales off-white, showing green iridescence; many long, thin, white cruciate hairs below AME. Chelicera shiny black in front and back; tips and fangs pale brown, with vestiture of white hairs, completely covering upper one-fourth, continuing around on sides to rejoin at tip. Sternum, labium, endites, coxae, and trochanters yellowish-white to slightly brownish-orange, unmarked. Abdomen with integument dark brown above, mottled; central light band diffuse and divided anteriorly, becoming solid behind middle, with chevron-like lateral extensions; integument laterally and ventrally pale, with patchy infuscations, especially in front of spinnerets and over lungs; vestiture of light (tan to white) scales ventrally and laterally; dark scales dorsally corresponding to dark integument; light central band overlain by white scales.

Legs with integument uniform yellow-orange to white, slightly dark above; femora I-IV, and patella and tibia I shading to dark brown above; leg I with femur and patella with dense posteroventral fringe of orange hairlike scales, reduced in density beneath tibia; same fringe on anterolateral face of same segments; telotarsus with integument dark, covered with black scales for whole length on all sides except dorsal; femur I with white scales above; other legs sparsely covered with white scales. Palpus with



Figs. 5-7.—*Pellenes kawini*, new species: 5, face; 6, ventral view of male palp; 7, retrolateral view of male palpal tibia.

Figs. 8-10.—*Pellenes kubai*, new species: 8, face; 9, ventral view of male palp; 10, retrolateral view of male palpal tibia.

integument of femur dark basally and dorsally, as are dorsal surfaces of patella and tibia; otherwise same yellow-white as rest of integument; tarsus covered with short, pale hairs, bulb as in fig. 6; tibial apophysis as in fig. 7.

Measurements.—Total length 4.235 mm; carapace length 2.1 mm; LOF 0.92 mm; WOF III 1.4 mm; clypeus height 0.33 mm; face height 0.66 mm; tibia I length 1.11 mm; basitarsus and telotarsus I length 1.7 mm; femur III length 1.7 mm; patella III length 0.925 mm; tibia III length 1.04 mm; femur IV length 1.51 mm; tibia IV length 0.925 mm.

Ratios.—A = 0.438, C = 0.5, D = 2.77, F = 0.789, H = 1.21, I = 1.12, J = 1.53, K = 0.666.

Female.—Unknown

Diagnosis.—*P. kawani* may be distinguished from other members of the *americanus* group except *Pellenes mustaciata* Chamberlin and Ivie by the shiny black anterior surface of the chelicerae, and may be distinguished from *P. mustaciata* in lacking a lateral extending "moustache" of clypeal scales, in having scales showing green iridescence on the clypeus (fig. 5), and in having telotarsus I black for its entire length.

Distribution.—Known only from type locality.

Pellenes (Habronattus) kubai, new species

Figs. 8, 9, 10.

Types.—Male holotype from 2 miles E. of Monitor Pass, Alpine Co., California, 8100', 10 July 1975 (C. E. Griswold), California Insect Survey, deposited on indefinite loan in the California Academy of Sciences. Paratopotype male, reared, in collection of author. The specific name is a patronym in honor of Stanley Kuba, who collected another specimen of this species at Leavitt Falls.

Male.—Carapace with integument dark brown, black on ocular area; covered with black scales, densest on ocular area; lower margin with thin band of scales beginning behind level of PLE and continuing to petiole; narrow band of white scales beginning behind level of PLE and continuing to petiole; narrow band of white scales beginning just behind AME and continuing back on ocular area to level of PME; on each side of ocular area a dense crest of long, black hairs originating between PME and ALE and extending forward to above AME (fig. 8). Clypeus covered with narrow, brown scales on upper part; lower part with two patches of iridescent blue scales on each side; oral margin with fringe of long orange scales. Chelicera with integument dark brown on anterior surface, light brown posteriorly, and palest near tips; covered above for 0.67 length by long, orange scales bordered with white scales (fig. 8). Labium and endite, dusky brown, tips pale; sternum, coxae and trochanters dusky brown. Abdomen with integument mottled with light and dark dorsally, thin light and dark lines laterally; venter pale yellow with three longitudinal dusky bands; dorsum covered with black scales; central longitudinal band of white scales on anterior part; and a second narrower band on posterior part, not quite reaching spinnerets; spinnerets dusky brown. Leg I with integument of femur dark brown on dorsal and anterior surfaces, light brown elsewhere; femur with sparse covering of thin black scales, forming a short posteroventral fringe distally; patella like femur but lacking fringe; integument of tibia, basitarsus and telotarsus dark on anterior and posterior surfaces, lighter dorsally and ventrally; tibia with appressed dark hairs dorsally, black scales anteriorly, and sparse

white scales ventrally; basitarsus with few dark hairs, and white scales ventrally; telotarsus with distal half densely covered with black scales except on dorsal surface; legs II-IV with integument like leg I; femur and patella II like leg I, except fringe smaller and scales on anterior surface brown to tan in color; telotarsus II pale; legs III and IV with sparse covering of black hairs and white scales, integument showing through plainly. Palpus with integument pale; femur with orange scales mesally, golden-brown scales ectally; patella same ectally, with fringe of yellow to white hairs mesally; tarsus heavily fringed with long white hairs ectally, shading to shorter golden hairs mesally; bulb typical of *americanus* group (fig. 9); tibial apophysis as in fig. 10.

Measurements.—Total length 4.44 mm; carapace length 2.28 mm; LOF 0.99 mm; WOF III 1.37 mm; carapace height 1.18 mm; face height 0.72 mm; clypeus height 0.38 mm; femur I length 1.52 mm; tibia I length 0.92 mm; basitarsus and telotarsus I length 1.86 mm; femur III length 1.86 mm; patella III length 0.91 mm; tibia III length 0.91 mm; femur IV length 1.44 mm; tibia IV length 0.91 mm.

Ratios (mean calculated from three males).—A = 0.40, C = 0.52, D = 0.76, F = 0.74, G = 1.06, H = 1.30, I = 1.25, J = 1.78, K = 0.59.

Female.—Unknown.

Diagnosis.—*P. kubai* may be distinguished from other members of the *americanus* group in having the chelicerae covered above with bands of closely appressed scales iridescent orange and white; in having the clypeus with patches of iridescent scales on lower half (fig. 8), and the palpi with fringes of long, white hairs.

Variation.—Paratopotype essentially identical to holotype. Male from Leavitt Falls, Mono Co., Calif., differs from the type as follows: central white band on ocular area absent, the crest over the anterior eyes solid and golden colored, the iridescent area of the clypeus forming a band rather than patches, the underparts pale yellow-white, and leg I with short fringe of white hairs beneath femur to tibia. A male from Lake of the Woods, Oregon, has a clypeus of the type form, but the crest solid and golden colored. There is a large range for all ratios calculated.

Note.—Males of *P. kubai* have the fringes on the palpus and first leg white in life. Living *Pellenes americanus* (Keys.) have these areas red, though these areas may fade to white after preservation.

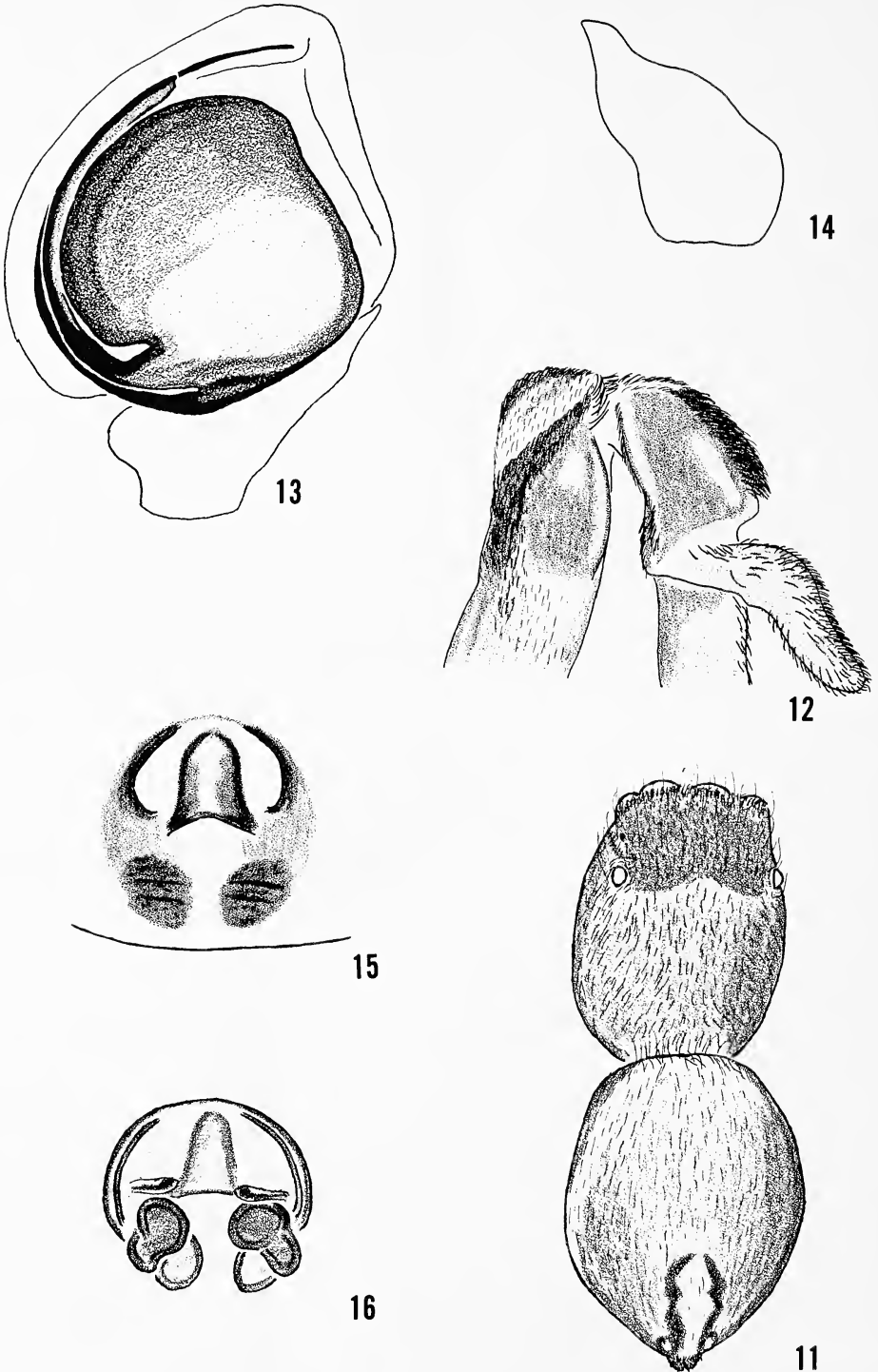
Natural History.—Specimens have been collected on the ground in Sagebrush Scrub at high altitudes. The closely related *P. americanus* has been collected in Yellow Pine Forest, Lodgepole Pine Forest, and Alpine Fell fields.

Additional Specimens Examined.—CALIFORNIA: *Alpine Co.*, 2 mi. E. Monitor Pass, 8100', one male, 10 July 1976, (C. E. Griswold, CEG); *Mono Co.*, Leavitt Falls, 3 mi. E. Sonora Pass, 8500', one male, 10 July 1975, (S. Kuba, CEG); OREGON: *Klamath Co.*, Lake of the Woods, 5000', one male, 1 to 4 July 1934 (Lawrence, AMNH).

Pellenes (Habronattus) schlingeri, new species

Figs. 11, 12, 13, 14, 15, 16.

Types.—Male holotype from Riverside, Riverside Co., California, "Ex cells of *Trypoxylon* sp.," 2 Sept. 1952, (E. I. Schlinger), deposited in the California Academy of Sciences. Paratopotypes, six females and two males: 1 male and 1 female in AMNH, the rest at UCR. The specific name is a patronym in honor of Evert I. Schlinger, who collected the types.



Figs. 11-16.—*Pellenes schlingeri*, new species: 11, dorsal view of female; 12, tip of femur and patella on third leg of male; 13, ventral view of male palp; 14, retrolateral view of male palpal tibia; 15, ventral view of female epigynum; 16, dorsal view of female epigynum.

Male.—Carapace with integument light brown, darker in ocular area and with a darker triangle on the posterior declivity, broadest at base and narrowing dorsally; ocular area thickly covered with short, closely appressed scales, iridescent gray; sides and thoracic region with dark brown scales, pattern of integument showing through; narrow band of white scales at lower margin; small fringe of tan to white scales above anterior eye row. Clypeus with silvery white iridescent scales from oral margin to bottom of AME, extending at this width past level of ALE onto side of carapace, diminishing width below PLE. Chelicera brown to yellow-brown, darkest at top; without covering of scales or hairs. Labium and endite dark brown, shading to white at tips. Sternum dark brown. Coxae and trochanters pale yellow, unmarked. Abdomen with integument obscured above by covering of scales; narrow light and dark longitudinal bands laterally reaching to base of spinnerets; venter pale, with infuscation near petiole, small infuscations near gastric furrow, and small, narrow infuscation in center midway between gastric furrow and posterior spiracle; covering of scales a narrow promarginal white band, and a second oblique white band extending just cephalad of middle on each side; narrow dorsal white spot just behind middle, and a small white spot on each side just before spinnerets; remainder of dorsum covered with narrow black scales; spinnerets dark gray dorsally, pale ventrally. Legs with integument yellow-brown, darker dorsally; telotarsi pale yellow; femur I with thick anterolateral fringes of long, thin, brown scales and posteroventral fringe of yellow-white scales, broadly flattened at tips; patella and tibia I with posteroventral fringe of short scales like those on femur; tibia I with two dark spatulate spines on anterior surface, at 1/3 and 2/3 distance from proximal end of segment; femur and patella III modified (fig. 12); distal surface of femur and middle surface of patella shiny dark-brown; femora II and IV with dorsal subapical infuscations. Palpus with all segments yellow-brown; tarsus with a few white scales but lacking fringes or tufts; tibial apophysis as in fig. 14; bulb typical of *coecatus* group (fig. 13).

Measurements.—Total length 4.36 mm; carapace length 2.32 mm; LOF 1.06 mm; WOF III 1.48 mm; carapace height 1.03 mm; face height 0.65 mm; clypeus height 0.23 mm; femur I length 1.33 mm; tibia I length 0.99 mm; basitarsus and telotarsus I length 1.29 mm; femur III length 1.79 mm; patella III length (less projection) 0.95 mm; tibia III length 0.95 mm; femur IV length 1.48 mm; tibia IV length 0.95 mm.

Ratios (calculated from 12 males, various localities).—A = 0.41 (0.38-0.43), C = 0.39 (0.35-0.47), D = 0.98 (0.88-1.08), F = 0.61 (0.58-0.69), G = 0.90 (0.86-0.92), H = 1.17 (1.07-1.25), I = 0.81 (0.67-0.90), J = 1.42 (1.19-1.50), K = 0.63 (0.60-0.65).

Variation.—Coloration of the tip of femur III and anterior surface of patella III varies from brown to black, always shiny.

Female (4 paratopotypes).—Carapace with integument of sides and thoracic region reddish-brown; ocular area dark brown; sides and thoracic region with uniform, sparse covering of long white scales; scales becoming shorter and denser on ocular area, with dark integument showing through to give area dark-brown or dark-gray to black, shiny appearance; long black hairs on ocular area, sparse at top of posterior declivity, more numerous near anterior eyes. Clypeus unmarked; covered with long, converging, cream to yellow scales, color varying with extent to which integument shows through; area below each AME darker; several pairs of long, white cruciate hairs above clypeal margin. Chelicera with integument light yellow-brown to dark brown, darkened at base; basal patches of white scales on anterior face present or absent. Labium and endite dark basally, shading to cream near tips. Sternum yellow to yellow-brown,

unmarked. Coxae and trochanters yellow to cream. Abdomen with integument solid gray to gray-brown dorsally, breaking up into narrow light and dark lines laterally; light spot or line beginning near middle and extending caudad to just before spinnerets; two small white dots just before spinnerets; venter pale yellow to cream, darker around spinnerets, and with dark line extending from epigastric furrow to posterior spiracle, covered dorsally with yellow to light brown scales; integument showing through to give a yellow-gray color; posterior line of white scales ending just before spinnerets, outlined in black; abdominal pattern as in fig. 11. Legs yellow-brown to dark brown; femora lightest on anterior surface near base, shading to darkest distally on dorsal surface; posterolateral surfaces of femora I and II with large, light blotches, coloration of other segments uniform; telotarsi lightest distally. Palpus pale yellow to yellow-brown. Epigynum as in fig. 15; spermathecae and associated internal structures as in fig. 16.

Measurements (9 females, Riverside and Winchester).—Total length 5.54 mm (6.93-4.31); carapace length 2.33 mm (2.55-2.07); LOF 0.98 mm (1.07-0.85); WOF III: 1.54mm (1.63-1.40); femur I length 1.15 mm (1.52-0.78); tibia I length 0.74 mm (0.81-0.62); femur III length 1.66 mm (1.81-1.40); patella III length 0.91 mm (1.04-0.74); tibia III length 0.86 mm (0.92-0.77); femur IV length 1.44 mm (1.59-1.25); tibia IV length 0.91 mm (0.96-0.77).

Ratios.—B = 1.06 (0.95-1.19), E = 1.07 (0.95-1.18), F = 0.47 (0.44-0.52), G = 0.77 (0.71-0.82), H = 1.07 (1.0-1.13).

Diagnosis.—*P. schlinger* belongs to the *coecatus* group. Males may be distinguished from those of *Pellenes coecatus* (Hentz) in having the clypeus covered with silvery white scales, and from the males of *Pellenes brunneus* Peckham, *Pellenes mexicanus* (Peckham), and *Pellenes captiosus* Gertsch in having both the top of femur III and anterior surface of patella III smooth and shiny brown, with the patellar projection thick and almost equal in length to the rest of the patella (fig. 12). Females may be distinguished from those of *P. coecatus* and *P. captiosus* in having the light patch on the dorsum of the abdomen narrow and restricted to the posterior part (fig. 11), and from *P. mexicanus* in having this posterior light spot solid rather than broken into chevrons. No characters are known for separation from the females of *P. brunneus*.

Natural History.—This species is frequently taken in urban or suburban situations, being common in lawns throughout the year in southern California. Additional habitat records are from the Coastal Sage Scrub community. Courtship behavior has been observed and differs in certain details from the closely-related *P. brunneus*. In specimens of *P. brunneus* from California the male approached the female with the palpi spread 90° to the sides, with the palpal tarsi above and outside the femora of the first legs, while in *P. schlinger* the palpi were spread only slightly, with the palpal tarsi inside the femora of the first legs and the bulb parallel to the sagittal plane of the body.

Distribution.—Northern Baja California and southern California along coast east to edge of deserts; north in Central Valley to San Joaquin Co., where it is sympatric with *P. brunneus*.

BEHAVIORAL RESPONSE TO WHOLE-BODY VIBRATION IN THE ORB-WEAVER *ARANEUS SERICATUS* CLERCK (ARANEAE: ARANEIDAE)

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ABSTRACT

Orb-weaving spiders of the species *Araneus sericatus* demonstrate a reflex among the first or second pair of legs in response to vibrational pulses delivered to the substrate. This response served as the dependent variable in determining the absolute threshold sensitivity to vibration. Sensitivity was best (smallest displacement amplitudes) in the region of 125 hertz. The reaction time of the response was inversely related to vibration intensity. The response occurred within 100 milliseconds for supra-threshold stimuli. This study confirms, by a behavioral method, the frequency response range of the orb-weaver as indicated in physiological research. Evidence is given which shows that *A. sericatus* can respond to acoustical stimuli at frequencies greater than about 300 hertz.

INTRODUCTION

The mechanical stimulation produced in the web by struggling prey may or may not provide distinctive signals for the orb-web spider. Impact and motion of prey seem to be the events which initiate the response; there appear to be no anticipatory movements stimulated by the wingbeat of approaching insects, although the effectiveness of sound as a stimulus has been established in several species of spider (Frings and Frings 1966, Walcott 1969). Moreover, the visual capacity of the orb-web spider is insufficient for the supposition that it plays any role in identifying the contents of the web.

There are several strategies in establishing the spider's mechanical sensitivity. One productive course is to measure the response of single neurons when legs are moved or vibrated (Finck unpublished, Walcott and Van der Kloot 1959) or when slit-organs are selectively stimulated (Barth 1967, Barth and Bohenberger 1978). It is probably, but not necessarily, the case that the mechanical sensitivity of the animal can be deduced from knowledge of the responses of individual nerve cells— assuming the sensory apparatus to have been accurately and completely identified. Not all investigators have been comfortable with that assumption and have attempted to assess sensitivity *in situ*, that is, with the spider exposed to nearfield and farfield vibration while in its web (Frings and Frings 1966, Walcott 1963). However, as Frings and Frings have pointed out (1966), it is difficult to

determine the precise characteristics of the stimulus as received by the spider at the hub. If vibration is applied to the catching zone of the web, for instance, the signals are attenuated and altered as they travel across the intervening network of threads.

We have chosen a third approach, in which the dependent variable is behavioral rather than electrophysiological, and in which vibration is applied to a solid substrate on which the animal is resting. Some of the limitations of the other approaches are avoided by this procedure, but on the other hand certain limitations of this technique have also to be borne in mind; they will be discussed in evaluating the results of the study.

METHOD

Vibratory stimuli were employed to elicit a motor response in female spiders of the species *Araneus sericatus* Clerck. We refer to this response as the vibratory motor response (VMR). It is a twitch of the first or second pair of legs. The movement is of brief duration and is not necessarily visible to the unaided eye, although it may be followed by gross movements as the animal retreats or readjusts its position.

In employing a behavioral measure, it is of course necessary not only that the stimulus be precisely specified, but that phenomena such as habituation be controlled. The motor response involved in the spider's dropping from the web, which the Peckhams (1887) and later Savory (1934) attempted to use in assessing vibratory sensitivity of orb-weavers, is complicated by progressive waning of the response with repeated application of the stimulus. A similar problem confronted Frings and Frings (1966) in using the spider's spasmodic extension of the first legs as an index of response to airborne vibration. The effects of habituation may be avoided by appropriate temporal spacing of trials. In the case of the VMR, we were able to establish by pre-testing that habituation could be avoided by spacing stimulation trials by at least 60 seconds.

The system for detecting and recording the VMR is shown in Fig. 1. The spider subject was placed in a translucent chamber mounted directly to a Pye-Ling V47 vibrator. A Sony video camera mounted on the side-arm of a Zeiss operating microscope delivered an image of approximately 17 X magnification to a TV monitor. Illumination was provided by a light source within the microscope. A photocell positioned over the image of the legs on the TV monitor detected minute movements of the legs. The photocell voltages were filtered (to remove the effects of the TV raster), amplified and permanently recorded on FM magnetic tape. A second tape channel recorded a timing pulse which marked the onset of the stimulus.

The stimulus consisted of a 300 msec pulse with a rise-decay time of 25 msec (thus voiding onset-offset transients). Stimulus amplitudes were controlled by attenuators matched to the impedance of the vibrator. Stimulus vibratory frequencies between 50 and 600 Hertz were delivered to the vibrator. Careful calibration was accomplished by the use of an accelerometer attached to the spider chamber and by direct, optical measurement. The vibration amplitude is reported in this study in decibels (dB) relative to a displacement of one micron. Thus, 0 dB=1 micron root-mean-square (rms), -10 dB= 0.316 micron rms and -20 dB= 0.1 micron rms. (The root-mean-square, an equivalent to the standard deviation of the peak displacement of a sine wave, has traditionally been employed to specify the amplitude of stimuli in studies of vibration).

The Vibratory Motor Response and Threshold Criteria.—The VMR served as the dependent variable for estimating the vibratory responsiveness of the spider. Fig. 2 shows the VMR for two animals at six different displacement levels and two frequencies. The response is clearly distinguishable from baseline variations. The duration of the response

varies between 100 and 200 msec (near the baseline). At vibrational intensities near threshold the VMR is often of smaller amplitude than at substantial suprathreshold levels, but the relationship between intensity and response amplitude is not sufficiently consistent to permit us to employ the vigor of the response as an indicator of sensitivity. On the other hand, the examples of the response shown in Fig. 2 demonstrate that response latency is related to the stimulus: reaction time decreases with increased vibrator displacement. On the TV monitor the VMR is seen as a minute lateral deflection of the first or second leg. The movement is probably similar to the reflex reported by Seyfarth (1978) in *Cupeinnius salei* Keys. Seyfarth found that it could be elicited by application of sinusoidal displacements to the tarsus, but he did not report the stimulus-response latencies.

The vibration threshold at a particular frequency was defined as that intensity which just evoked a VMR. Our procedure was to deliver stimuli in ascending steps according to a Method of Limits. The first stimulus was presented well below the estimated threshold and increased in amplitude by five decibel steps until the VMR appeared. The response was confirmed by increasing the amplitude of the vibrator another five dB. In order to exclude responses not contingent upon the stimulus, a time-window of 2.5 secs was set. Leg movements which occurred with latencies exceeding this interval were not considered responses. Sometimes a spontaneous movement occurred just before the delivery of a stimulus: those trials were excluded.

RESULTS

The results are based upon the responses of 22 spiders given a total of 823 trials at 14 different vibration frequencies. The response region for the species was calculated by tabulating the attenuation values obtained at threshold. Having determined the proportion of responses from all the animals at a given level, we converted the attenuation levels (relative dB) into displacement according to our calibration of the Pye-Ling vibrator.

Figure 3 shows the thresholds for the total sample of animals. The ordinate is given in decibels re: 1 micron rms. Thus zero dB represents a 1 micron displacement and + 20 dB a 10 micron displacement. Vibration frequency (in Hz) appears on the abscissa. The two curves in the figure represent the median threshold value (half of the animals required greater, half smaller displacement to produce the threshold response) and the 75th percentile (75 percent of the animals required greater displacement to reach threshold and 25 percent required smaller).

The median (50 percent) results (closed circles) show an increasing sensitivity between 50 and 125 Hz and a rapid decrease for frequencies exceeding 125 Hz. The 75th percentile curve (open circles) demonstrates an overall lower absolute threshold because it employs a more liberal criterion for definition of threshold. Together these results indicate that the best amplitude sensitivity for the animals is between 125 and 150 Hz.

An inevitable feature of a vibrator, especially when it operates at a substantial level, is to produce sound. In assessing sensitivity to movement of the substrate, it is necessary to exclude sound as a possible stimulus. Figure 3 contains, on the right, data points not joined to their appropriate (median or 75th percentile) curves. They represent thresholds for frequency locations at which the spider was apparently responding to sound rather than to direct vibration. This condition was established by retesting 5 of the 22 animals while exposed to a continuous acoustic noise. Specifically, a 90 dB (re: 0.0002 microbar) white noise was delivered to the spider chamber while vibration thresholds were repeated

in the usual manner. This acoustic masking noise had no observable effect on thresholds taken below 300 Hz, but stimuli above 300 Hz, which had previously been effective in eliciting the response, did not do so in the presence of the masker.

Figure 4 shows response latency (reaction time) of the VMR as a function of vibration intensity. The ordinate represents time (in msec) from the onset of the stimulus to the peak amplitude of the VMR (see Fig. 2). The abscissa represents the displacement of the stimulus in terms of attenuation. For example, -25 dB is a stimulus displacement 0.56 times smaller than zero dB, and -10dB is a displacement 0.316 of the displacement at zero dB. These data demonstrate that when the intensity of the stimulus is increased the reaction time of the VMR decreases. The response latency curves are non-linear and they tend toward an asymptote at the higher stimulus intensities (i.e. the smaller attenuation values). The dynamic range (intensity sensitivity) is seen to be at least 15 dB for most of the spiders. One animal shows a very restricted range of sensitivity, about 5 dB. The reaction times of the VMR were measured to the peak of the response with some of the shortest latencies occurring in the region of 100-200 msec. Of course, reaction times measured from the very first indication of a response would have yielded lower values; in several of the animals such latencies would have been much less than 100 msec.

DISCUSSION AND CONCLUSIONS

Our results demonstrate that the sensitivity of *A. sericatus* to substrate vibration ranges from at least 50 Hz to about 200 Hz. In the region of 125 Hz the threshold amplitude is near 10 microns displacement (75th percentile curve). Electrophysiological research has described lower displacement thresholds.

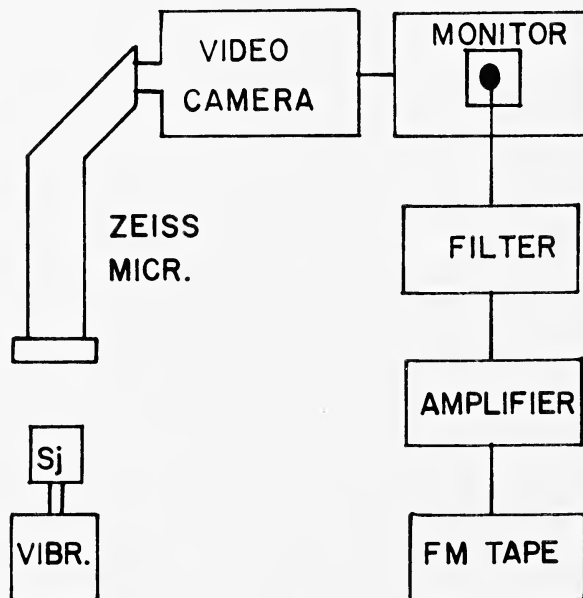


Fig. 1.—Schematic diagram of the recording system. The spider chamber (S_j) is mounted directly on the vibrator (VIBR.). A photocell (black circle), positioned at an aperture in an opaque shield is placed on the enlarged video image of the leg. Small movements of the legs change the relative intensity of the light, producing changed photocell voltages which are filtered, amplified and recorded.

Walcott and Van der Kloot (1959) studied threshold sensitivity in *Achaearanea tepidariorum* with electrophysiological techniques. They reported thresholds of about 0.025 microns at 2000 Hz. Finck (1972) also employed an electrophysiological measure for the determination of sensitivity in *Araneus diadematus*. His results indicated that frequency sensitivity was best in the region of 90-150 Hz. This is a frequency region which corresponds to the behavioral sensitivity of *A. sericatus* (present study). Finck (unpublished results) has also recorded from single neural units in the leg ganglia of *A. sericatus*; these unit thresholds indicate a best frequency region of 90-125 Hz with occasional thresholds as low as 0.22 microns but with most requiring at least 30 microns displacement.

The behavioral thresholds reported in the present study are of the same order of sensitivity as the majority of single unit thresholds in the same species. However, as indicated above, a few single neurons may demonstrate considerably smaller displacement sensitivities.

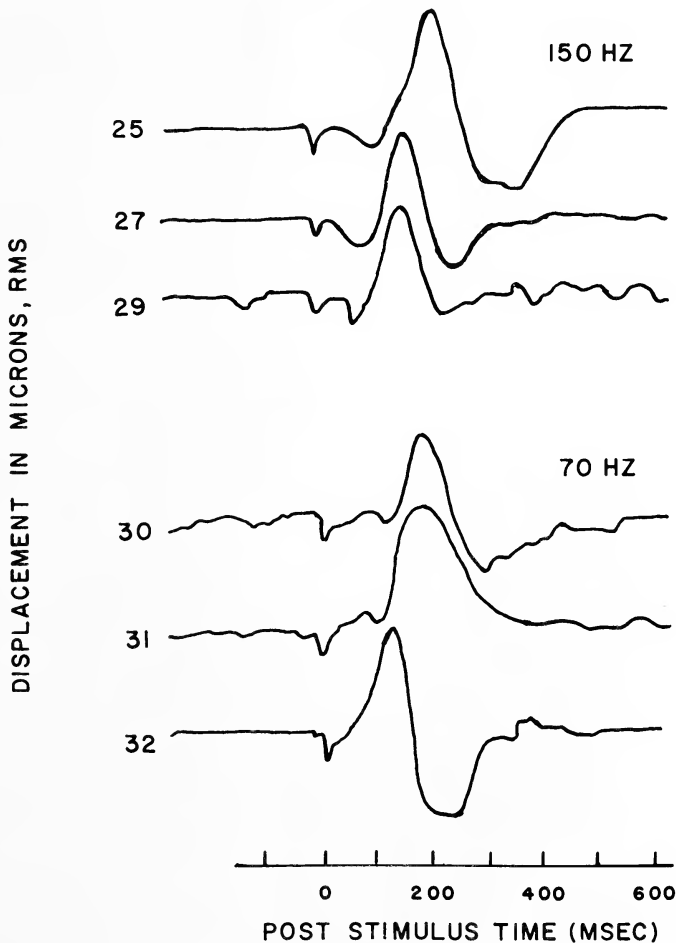


Fig. 2.—Vibratory motor response (VMR) at increasing stimulus amplitudes at two frequencies. The ordinate represents vibrator displacement in microns for stimulus frequencies of 70 and 150 hertz. The tracings record changes in position of a leg following the onset of a 300 msec pulse at time zero on the abscissa.

In evaluating this finding, we may consider the relative roles of acoustic and substrate vibration. A spider's response to sound has been observed and studied by several investigators (Barth 1967, Frings and Frings 1966, Peckham and Peckham 1887, Walcott and Van der Kloot 1959). We were able to separate the direct-vibration component from the sound-induced component of the sensitivity curve by introducing a masking noise. This masking noise obviated the effect of stimulus frequencies above 300 Hz. That is, in the presence of the masker, vibration of the substrate for these frequencies was ineffective in producing responses. Thus sensitivity to direct-substrate vibration does not appear to extend above 300 Hz. Consequently it is possible that the exquisite sensitivity of the spider to higher frequencies may be due to sound in the near field.

It may well be the case that the lyriform organ transduces both direct vibration and acoustic energy. Some evidence for that possibility is given in the research of Barth (1967), who demonstrated that a single slit-sense organ in *Cupiennius salei* could respond to sound stimuli. Walcott and Van der Kloot (1959) also demonstrated that the excised leg of *A. tepidariorum* was sensitive to both sound and vibration. Our results indicate that

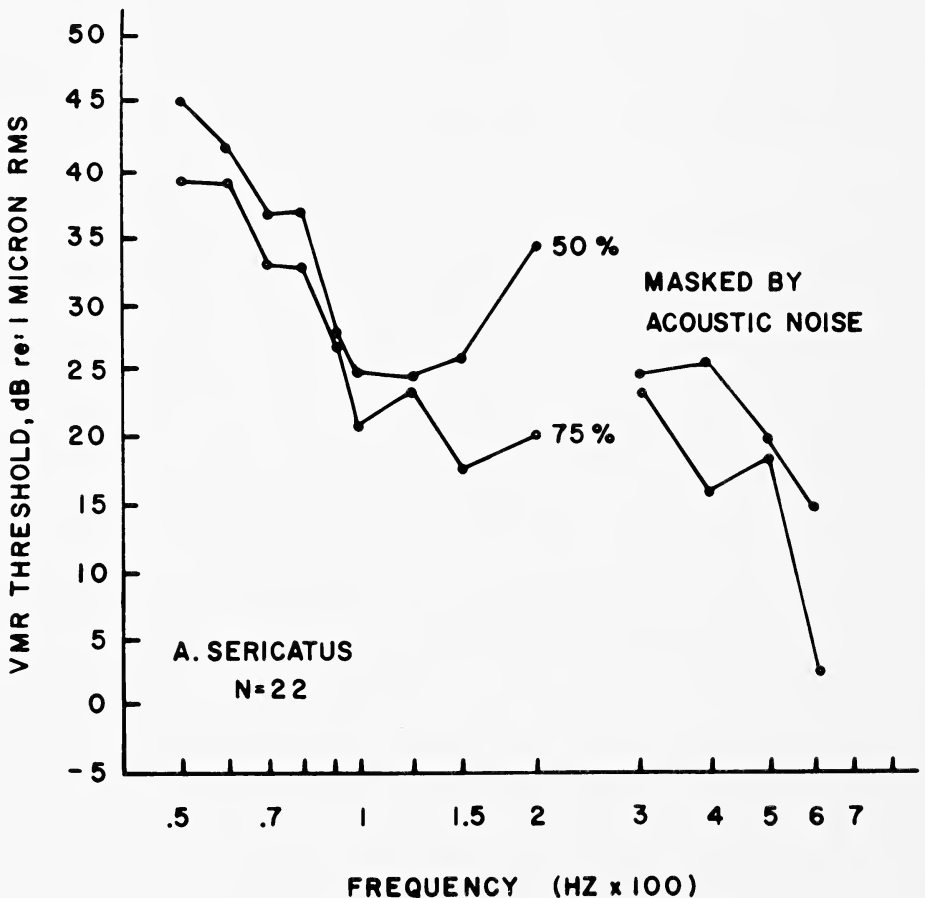


Fig. 3.—Vibration threshold as a function of frequency. The ordinate is stimulus displacement in dB where zero dB equals 1 micron. Frequencies "masked by acoustic noise" show thresholds obtained only in the absence of a 90 dB acoustic noise.

in the acoustic region of *A. sericatus* (300 Hz and higher) threshold displacement decreases rapidly (see Fig. 3, region marked "Masked by Acoustic Noise"). This finding is precisely what would be expected for sound waves in the near field: an inverse relationship between displacement amplitude and frequency. Therefore for *A. sericatus* the region of 300 Hz appears to be a kind of demarcation point above which acoustic pressure alone is the salient stimulus dimension.

It is still possible only to speculate on the relationship between vibration sensitivity in the orb-weaving spider and the production of vibro-acoustic stimulation by insects captured in the web. Little is known about the web as a transmission link between the source of vibration and the spider, although Walcott (1963) has shown that single strands of spider silk (taken from *A. tepidariorum*) can transmit vibrations from about 50 to 2000 Hz. He also found that the attenuation of vibratory displacement is only about 1.2 to 1.5 dB per centimeter of thread, a finding which would make the thread an efficient substrate for the transmission of vibrations to the spider. However, there may be some danger in generalizing this observation to vibratory characteristics of the whole web,

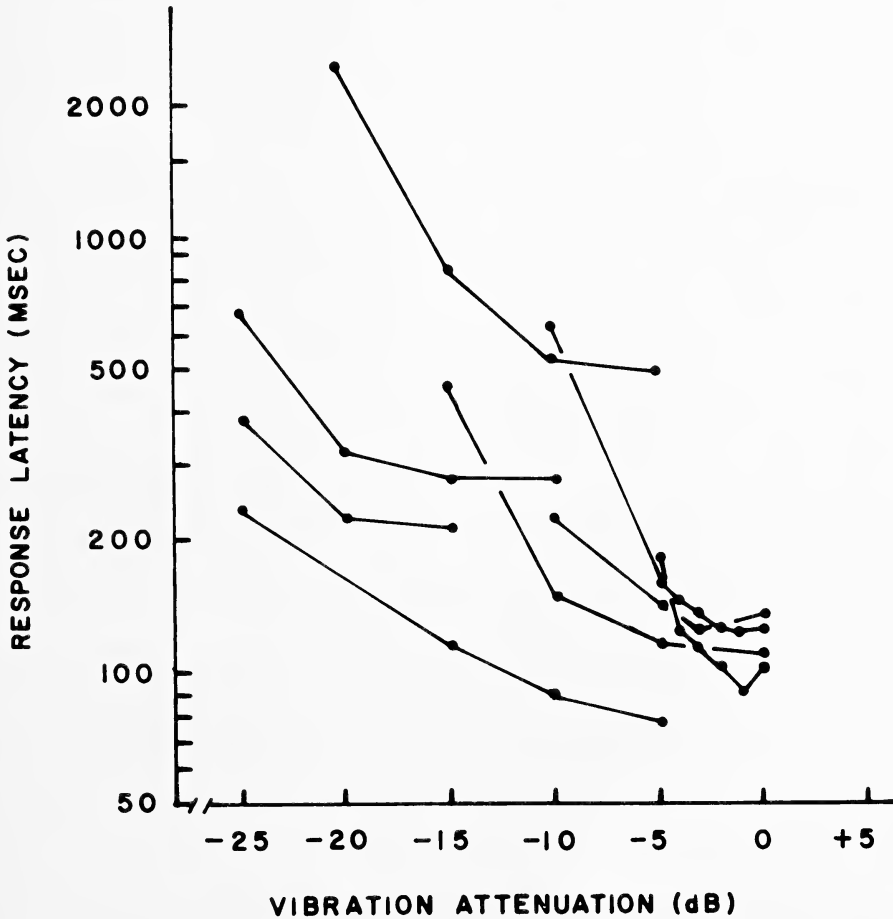


Fig. 4.—Latency of the VMR as a function of vibration amplitude (8 animals). Latency is measured from the onset of the stimulus to the peak amplitude of the response. The abscissa shows attenuation (relative vibration amplitude) in decibels.

which is a complex, interconnected structure, and which can vary in its parts in tension, thickness of thread, and mode of attachment, to name only a few variables.

Further, there is to our knowledge no report on the generation of web vibration as opposed to acoustic pressure by insects ensnared in the web. Walcott (1969) did report on the honey bee and the house fly as acoustic sources in the near-field when snared. In these observations the main acoustic energy peaks were located at about 700 Hz for the house fly and at two peaks of 500 and 2000 Hz for the honey bee. These represent acoustic frequencies well above the vibratory sensitivity of *A. sericatus* as found in the present study and for *A. diadematus* (Finck 1972). Nor does it appear that the web acts to convert pressure waves at acoustic frequencies into web motion and thus vibration to which the spider could respond. Finck, Stewart and Reed (1975) studied the resonant characteristics of the web of *Araneus diadematus* Cl. in a sound field. Their results showed that even in relatively intense sound fields (+90 dB re: 0.0002 microbar) web movement peaked near 25 Hz with virtually no movement for other frequencies between 20 and 20,000 Hz. The orb web of that species, and probably of other species with webs of similar geometry, cannot serve as an acoustic detector for the approach of flying insects with wing beats exceeding 25 Hz. To the extent that *A. sericatus* employs only the direct vibratory system described here, it is largely isolated from distant sound sources. At least as a detector of direct vibration, it is restricted to rather low frequencies.

Finally, some comments must be made on the utility of the present procedure. While it furnishes specifiable, direct stimulation, and avoids some complications of testing the animal in the web, it is well to keep limitations in mind. The legs and body are directly vibrated, but are not in the posture characteristic of the spider hanging in the web. It is very possible that the posture represents an optimal positioning of receptors and accessory structures, or may provide ready adjustment in order to enhance sensitivity, for instance by extending the legs. Walcott and Van der Kloot (1959) had reported that, in *A. tepidariorum*, frequency response could be altered by changing the position of a leg. Finck (unpublished data) was unable to confirm that result for *A. sericatus* but did find that thresholds at a given frequency could be improved by altering the position of the leg. It may be the case that the spider can, by positioning its legs, exert control over the sensory input; this possibility remains to be demonstrated.

ACKNOWLEDGEMENTS

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DIET AND FEEDING PHENOLOGY OF THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE: OXYOPIDAE)

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ABSTRACT

Natural diet of the oxyopid, *Peucetia viridans*, was analyzed over a ten month period. This spider is a euryphagous predator; of the 189 prey items recorded in the field there were 65 species of prey. Major diet items included species of Hymenoptera, Diptera, Hemiptera, Lepidoptera and Orthoptera. Conspecifics represented the fourth major prey species, but interspecific predation was found to be relatively rare. Phenological analysis of prey composition indicates that there is a large change in major prey taxa with time. Monthly prey composition probably reflects relative prey availability. The percent of adult males feeding in the field was not significantly different from that of adult females. Prey size exhibited a highly significant correlation to predator body size.

INTRODUCTION

Only in recent years has the role of spiders as important components of arthropod communities been recognized, and considerable interest has been displayed in the analysis of spider predation in natural ecosystems (Moulder and Reichle 1972, Riechert 1974). Knowledge of actual diet for a particular species of spider is a primary requisite before the impact of spider predation on arthropod communities can be correctly assessed. However, with the exception of studies by Kajak (1965), Turnbull (1960), Edgar (1969), Yeargan (1975) and Jackson (1978), relatively little in-depth, quantitative field work has been conducted on spider prey.

The data presented here resulted from a study on the patterns of species co-existence in a guild of raptorial spiders (Turner and Polis, 1979) which included four species of Thomisidae and one species of Oxyopidae, *Peucetia viridans* (Hentz). It is the purpose of this paper to 1) examine the natural diet of the oxyopid, *P. viridans*, 2) investigate the feeding phenology of this spider, and 3) ascertain if a correlation exists between predator size and prey size.

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NATURAL HISTORY

The green lynx, *P. viridans*, is a large, non web-spinning spider with long, conspicuously spinose legs (Kaston 1972). This species lives among low bushes and herbaceous vegetation and adult females can often be found on flowers where they lie in ambush for potential prey. Once a food item has been captured the spider retreats down into the vegetation or to the underside of the flowerhead to consume its prey. Spiders digest their prey externally in a process which often lasts several hours. Thus, analysis of prey is facilitated as the prey exoskeleton is often left intact and can be identified.

Male lynx spiders wander during the mating season which runs from May through July in California (Icenogle, personal communication). Beginning in late June, fertilized females attach their eggsacs to the vegetation and remain with the sac until after the spiderlings have emerged. Once the young hatch they stay close to the eggsac (Whitcomb et al. 1966, personal observation), and disperse seven to ten days after emergence. Under California field conditions, the female can construct more than one egg sac. I often observed new eggsacs attached to older, empty eggsacs as late as December.

METHODS AND MATERIALS

The study was conducted over a ten month period (March to December, 1977) in a dry coastal sagebrush area immediately adjacent to the eastern border of Lake Perris State Park in Riverside County, California. The dominant vegetation is composed of several species of low (<1.5m) perennial shrubs: *Eriogonum fasciculatum* (Benth), *Artemesia tridentata* Nutt., *Encelia californica* Nutt., *Aster* sp., *Xanthocephalum californicum* (Greene), and one species of annual herb, *Brassica nigra* L.

Because *P. viridans* often blends cryptically with the plants it inhabits, surveys were carried out by systematically searching all vegetation in the area. At least four surveys per month were carried out. However, during the warmer months (e.g., July) up to eleven surveys per month took place. Observations of spider predation were made between 0900 hrs and 1800 hrs. When a spider was observed with a prey item, both the spider and prey were placed into a vial and preserved with 70% ethanol. Specimens were returned to the laboratory for measurement and prey identification.

Carapace width and raptorial leg length of each spider were measured to determine if correlations existed between predator size and prey length. Following precedent set by Dondale (1961) and Whitcomb et al. (1966), carapace width (rather than body weight or volume) was measured ($\pm 0.1\text{mm}$) with an ocular micrometer as an indicator of body size. Prey length and raptorial leg length of each spider were measured ($\pm 0.5\text{mm}$) with a standard metric ruler. In total, 189 prey items were recorded from the field.

To determine relative feeding specialization, niche breadth of prey species was calculated for *P. viridans* using Levins' (1968) method.

RESULTS AND DISCUSSION

Diet.—A list of the prey species taken by *P. viridans* (Table 1) indicates that this spider is a euryphagous predator, an observation which has been noted for a number of other spider species (Turnbull 1960, Moulder and Reichle 1972, Jackson 1978). By far the

Table 1.—Prey species of *Peucetia viridans*. The number in parentheses after a family name refers to the number of species recorded.

	No.	% of Total		No.	% of Total
Hymenoptera			Hemiptera		
Apidae			Coreidae (1)	2	1.06
<i>Apis mellifera</i>	26	13.76	Lygaeidae		
other species (3)	5	2.65	<i>Nysius</i> sp.	5	2.65
Anthophoridae (2)	5	2.65	other species (1)	1	0.53
Colletidae (1)	1	0.53	Miridae (2)	2	1.06
Chrysididae (1)	1	0.53	Nabidae (1)	1	0.53
Formicidae (1)	1	0.53	Pentatomidae (1)	2	1.06
Megachilidae (1)	1	0.53	Reduviidae (1)	3	1.59
Pompilidae (3)	5	2.65	Rhopalidae (1)	1	0.53
Halictidae			Coleoptera		
<i>Dialictus microlepoides</i>	8	4.23	Chrysomelidae (1)	2	1.06
other species (9)	10	5.30	Melyridae (2)	5	2.65
Sphecidae (9)	10	5.30	Lepidoptera		
Vespidae (1)	3	1.59	Pieridae		
Unknown family (2)	2	1.06	<i>Pieris protodice</i>	25	13.23
Diptera			Hesperiidae (1)	1	0.53
Bombyliidae			Noctuidae (1)	1	0.53
<i>Bombylius</i> sp.	7	3.70	Unknown family (1)	1	0.53
other species (5)	7	3.70	Orthoptera		
Bibionidae (1)	1	0.53	Acrididae		
Calliphoridae (1)	1	0.53	<i>Melanoplus cinereus</i>		
			<i>cyanipes</i>	13	6.88
Syrphidae (3)	3	1.59	other species (2)	3	1.59
Tachinidae (4)	8	4.23	Araneae		
Chloropidae (1)	1	0.53	Oxyopidae		
Stratiomyidae (1)	1	0.53	<i>Peucetia viridans</i>	11	5.82
			Salticidae (1)	1	0.53
			Thomisidae (1)	2	1.06
			Total	189	

greatest number of diet items were species of Hymenoptera with *Apis mellifera* L. constituting the single most important prey taxon. Diptera were the second most numerous diet items and were represented primarily by species of Bombyliidae and Tachinidae. The cabbage butterfly, *Pieris protodice* L. comprised a significant proportion of the diet along with spur-throated grasshoppers (s.f. Cyrtacanthacridinae). However, no cases of feeding on lepidopteran larvae were observed although the larvae commonly occurred in the vegetation inhabited by *Peucetia*. In a study of the prey of *Pardosa ramulosa* (McCook), Yeargan (1975) also found that despite their abundance in the study area (alfalfa fields), larvae of Lepidoptera constituted only a small fraction of the diet. Although species of many Hemipteran families were eaten, one-third were represented by small seed-bugs from the family Lygaeidae.

Very few Coleoptera were used as prey, yet many species of beetles were present on the shrubs in the study area. This may be because the coleopteran cuticle is too hard to be penetrated by the spiders' chelicerae. The major group of beetles which were fed upon (Myrmelidae) are considered (Borror and DeLong 1971) to be soft-bodied species associated with flowers.

A number of previous studies have concluded that the most important predators of spiders are other spiders (Bristowe 1939, Edgar 1969, Yeargan 1975, Jackson 1978). In a study of the wolf spider, *Lycosa lugubris* (Walckenaer), Edgar (1969) found that 16% of the prey consisted of smaller members of their own species. Spiders represented the second most frequent diet item of *Phidippus johnsoni* (Pekham and Pekham) (Jackson 1978). Other spiders (particularly conspecifics) comprised a major portion of the diet for *Pardosa ramulosa* (Yeargan 1975).

During this investigation spiders contributed 7.4% to the total diet for *P. viridans*. A total of 14 spiders were recorded as prey items; three involved interspecific predation and eleven were cases of intraspecific predation. Overall, conspecifics represented the fourth major prey species. Most cases of cannibalism were of mature females preying either upon mature males ($n=7$) or immature spiders ($n=3$). The one case of cannibalism not involving a female predator was a penultimate male feeding on an immature individual. Although female lynx spiders stay with their young after emergence from the eggsac, no cannibalism was observed to occur near the nest site. However, females were observed to feed on insect prey during this period.

Feeding phenology.—Figure 1 depicts the proportion of major (most frequent) prey items taken through time. In the three month period from March to May the only prey observed to be taken were small flies (about 4 mm). Hymenopterans made up the largest proportion of prey in June and September. In July there was a decrease in the proportion of Diptera, Hemiptera and Hymenoptera; species of Lepidoptera, Orthoptera and Araneae first appeared in the diet. It is interesting to note that during the month of August there was a significant increase in the proportion of spiders in the diet and a relatively low proportion of insect prey. This fact may be correlated to an overall decrease in insect availability.

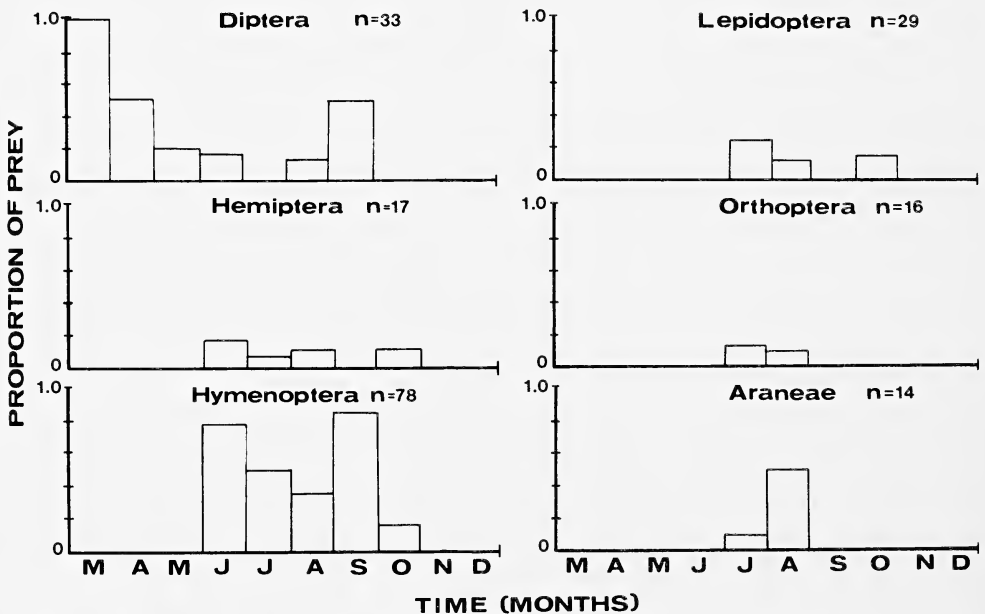


Fig. 1.—Percent of prey items taken monthly by *Peucea viridans*. All data were collected in the field from March to December. Only the most common prey orders are shown. n represents the number of prey items of each order.

Sex specific prey analysis.—Turnbull (1962) found that mature males of *Linyphia triangularis* (Clerck) did not require food in the adult stage while adult females fed normally. From observation in the laboratory and field, Jackson (1978) also concluded that adult males of *P. johnsoni* fed less frequently than females. He correlated this finding to the life style of adult males which is concerned primarily with locating females and mating. Data obtained during the present study for *P. viridans* would initially appear to confirm the hypothesis that adult males feed less often than adult females. Only twelve mature males were observed with prey as compared to 131 mature females. However, relative to the total number of adult males censused in the field, the percent feeding (21.4%) was non-significantly higher than that of adult females (20.4%) (t test for difference in proportions: $t=0.03$, $p>0.5$). Therefore, this analysis suggests that per capita feeding rather than simple totals should be the criteria for feeding rates.

To determine if a correlation exists between predator and prey characteristics, prey length was analyzed as a function of body size (carapace width) and raptorial leg length. Significant positive correlations were obtained for both morphological features, with body size (Fig. 2) showing a higher correlation ($r=0.496$, $p < 0.001$). Thus, it appears that in the case of *P. viridans*, larger spiders take larger prey.

Niche breadth along a particular resource dimension such as food type is inversely related to ecological specialization. The smaller the niche breadth of an organism, the more specialized it is. Using Levins' method (1968) the niche breadth of prey species for *P. viridans* was calculated. A significantly high value ($\beta=3.58$) was obtained indicating that this spider is a generalist in the prey species it takes.

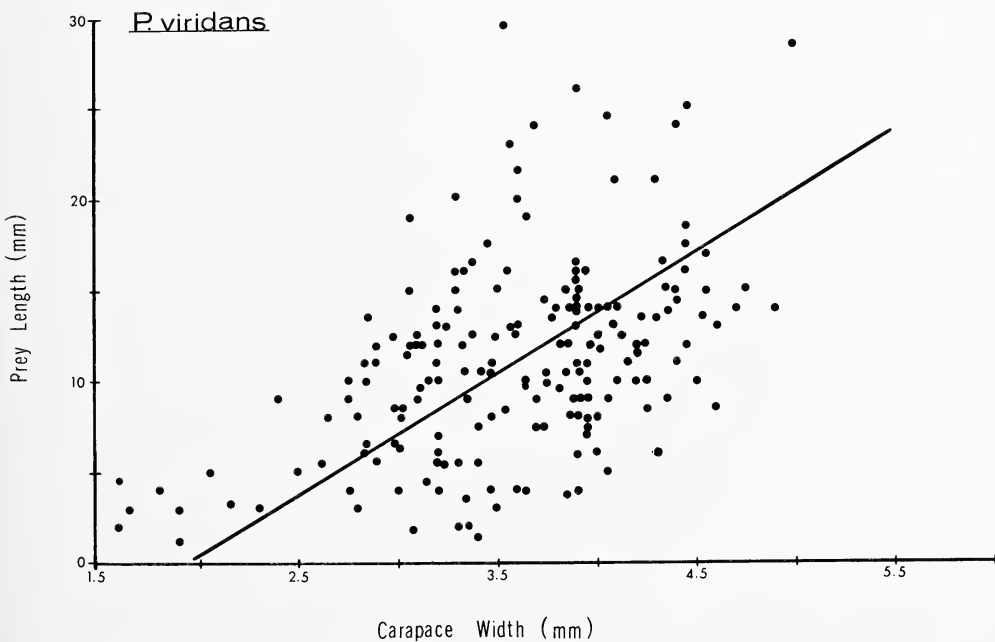


Fig. 2.—Prey length as a function of predator (*Peucetia viridans*) carapace width. There is a significant correlation ($r=0.496$, $p < 0.001$) between spider size and prey size. Equation for the regression line: $y = -2.27 + 0.496x$.

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PARAMETERS AFFECTING THE HABITAT CHOICE OF A DESERT WOLF SPIDER, *LYCOSA SANTRITA* CHAMBERLIN AND IVIE

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ABSTRACT

1. This study discusses a complex habitat selection strategy exhibited by a hunting spider species, the wolf spider *Lycosa santrita*, occupying desert riparian habitats in southeastern Arizona.

2. Field censuses of spider activity on various substrates show that significant associations exist between spiders and grass. This substrate provides the most predictable energy investment in prey capture of all natural substrates in the study area.

3. Mature spiders show less association with grass than younger spiders. Upon maturing, females move from the woodland area where grass is prominent to patches of bare ground and rock bordering a creek. Adult males also leave the woodland and settle in patches of leaf litter adjacent to the creek bed.

4. Available prey is shown to be highest on the bare ground substrate. As prey numbers were not found to differ significantly on any substrate through time, location changes made by adult spiders cannot be a reflection of temporal changes in local prey abundance.

5. We conclude that mature females require the greater numbers of prey afforded by the bare ground substrate for reproduction.

6. Mature male spiders move to the area of the creek bed in response to the presence of females in the area. Here the probability of mating is highest.

INTRODUCTION

To be a successful contender for resources an organism must employ a strategy which takes it to maturity and supplies its offspring with sufficient energy to initially compete for resources. One aspect of such a strategy is habitat selection which has been demonstrated to affect the fitness of spiders in various ways. For instance, it is considered by several workers to reduce interspecific competition within spider communities (Luczak 1966, Kessler-Geschiere 1971, Tretzel 1955, Gertsch and Riechert 1976, Post and Riechert 1977). Spiders have also been shown to escape thermal stress and maximize time for feeding activity by the selection of favorable microenvironments (Riechert and Tracy 1975, Riechert 1976).

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Few studies have dealt with habitat selection in the more active hunting spider species. An important contribution has been made by Greenquist and Rovner (1976) who showed that two temperate wolf spiders (Lycosidae) exhibit stratum preferences. The present study was instigated by field observations of a desert wolf spider, *Lycosa santrita* Chamberlin and Ivie. These observations suggested that this spider might utilize natural substrates which enhance its hunting activities. The study reported here was initiated to test this hypothesis and to determine whether *L. santrita* might also be maximizing its prey capture efficiency through selection of favorable substrates.

LYCOSA SANTRITA

Lycosa santrita is a prominent member of the spider communities of creek bank habitats in the Chiricahua Mountains of southeastern Arizona. This large wolf spider (16-20 mm in length), like most lycosids, does not build a web trap. Prey are detected visually and through vibrations monitored by tarsal slit organs and trichobothria (Barth 1967, Gorner and Andrews 1969). Further, prey is subdued without the use of silk. *L. santrita* remains stationary while locating prey and can be considered a sit-and-wait or ambush predator. In this respect, it is similar to those spiders which utilize webs in capturing prey.

STUDY AREA

The study was conducted in a desert riparian habitat on the grounds of the Southwestern Research Station of the American Museum of Natural History, Cochise Co., Arizona. The creek traversing this habitat has running water throughout the year. Mottled shade is provided by *Platanus wrightii* (Arizona sycamore) and *Acer negundo* (box elder); the floor of this woodland is predominantly grass. A more complete description of the vegetation of desert riparian habitats is available in Lowe (1972).

CAPTURE EFFICIENCY

Optimal foraging includes parameters related to: 1) food choice, 2) patch choice, 3) time allocation between different patches and 4) patterns and speed of movement (Pyke et al. 1977). We are concerned here with patch choice (i.e., the possibility that spiders might limit their hunting activities to specific substrates).

Although animals commonly select "patch" types according to the prey they offer (kinds and numbers), few examples of patch choice based on capture efficiency are available (See for example Bell 1971, Greenquist and Rovner 1976). The following experiment was designed to determine what effect, if any, substrate has on the capture success of *L. santrita*.

Methods.—Feeding experiments were conducted in plexiglass boxes (34.5 x 35 x 15.5 cm) each containing a different substrate type (i.e., rock, leaf litter, grass, or bare ground). (Grasshoppers are favored prey of this species population). Spiders chosen for a specific run had not been fed for at least 3 days.

Ten replicates were run for each substrate type using a total of 13 female and 15 male spiders. Two estimates of capture efficiency measured in the experiment were: 1) distance between the spider and the prey at the time of spider orientation towards the prey, and 2) the time between spider orientation and actual prey capture. In addition to substrate

the following factors were measured for each run: the size of the spider relative to that of the prey, resting heart rate of the spider and its temperature. Total body length and anterior width were used as a size estimate for prey, and cephalothorax and abdomen lengths and widths were used as spider size estimates; these were measured with a millimeter rule. Heart rate was estimated via the laser-illumination method described in Carrel and Heathcote (1976), and spider temperature was assumed to be equivalent to air temperature within the chamber (Riechert and Tracy 1975).

Results.—Once a spider detected, oriented towards, and then jumped forward to a prey in the experiments, it was always successful in the capture of that prey regardless of the substrate provided. Before considering the effects of substrate on the spider's ability to detect prey or on its capture time, it was necessary to correct the data for confounding by the various covariates listed above. Thus, analyses of covariance with multiple covariates (Bennett and Franklin 1954) were applied to the data (Table 1). A Duncan's multiple range test (Snedecor and Cochran 1967) was then used to test for differences existing among the substrates in corrected mean values of both distance and time (Table 2).

Table 1a.—Covariate statistics related to error within distance treatments. (r = regression coefficient, SE = standard error, t = t -value).

Covariate	r	SE	t	Tabular t
CEW	-3.3283	7.7409	-0.4300	$t_{(35,0.2)}=0.85$ $t_{(35,0.1)}=1.31$
CEL	6.1004	5.1407	1.1867	
ABW	-12.7210	6.8594	-1.8584	$t_{(35,0.2)}=0.85$ $t_{(35,0.3)}=0.53$
ABL	2.4140	4.9856	0.4842	
PRW	-11.6497	12.1564	-0.9583	
PRL	1.6844	2.4844	0.6780	
TEMP	-0.1859	0.6840	-0.2717	
HTBT	-0.0656	0.2257	-0.2905	
DOFI	0.0315	0.6868	0.0459	
DWFD	0.0585	0.7482	-0.0782	

Table 1b.—Covariate Statistics Related to Error within Latency Treatments (CEW = cephalothorax width, CEL = cephalothorax length, ABW = abdomen width, ABL = abdomen length, PWR = prey anterior width, PRL = prey length, TEMP = air temperature at time of capture, HTBT = resting heart rate of spider, DOFI = number of days since capture, DWFD = number of days since last feeding).

Covariate	r	SE	t	Tabular t
CEW	54.4964	79.8977	0.6821	$t_{(35,0.3)}=0.53$
CEL	7.7716	53.0598	0.1465	
ABW	-8.3161	70.7993	-0.1175	$t_{(35,0.3)}=0.53$
ABL	-21.1121	51.4592	-0.4103	
PRW	-106.3960	125.4729	-0.8480	
PRL	6.0850	25.6431	0.2373	
TEMP	7.8239	7.0509	1.1082	
HTBT	-2.5939	2.3297	-1.1134	$t_{(35,0.2)}=0.85$
DOFI	-5.6180	7.0886	-0.7925	$t_{(35,0.3)}=0.53$
DWFD	-5.7729	7.7226	-0.7475	$t_{(35,0.3)}=0.53$

Table 2.—Results of Multiple Range Tests [Underlined values are not significantly different from each other ($P > 0.05$)].

a. For Adjusted Orientation Distance:

Statistic	Substrates			
	Grass	Rock	Litter	Bare Ground
Adjusted Treatment \bar{X} (mm)	51.1	42.1	41.0	40.5

b. For Adjusted Time:

Statistic	Grass	Rock	Litter	Bare
				Ground
Adjusted Treatment \bar{X} (sec)	25.4	71.1	90.8	254.8

Substrate was not found to significantly affect either the spider's ability to detect prey at certain distances nor its capture time. However, significant correlations were observed in the relationship existing between detection distance and capture time (Table 3). This relationship can be considered a reflection of predictability of energy investment—the more linear the relationship, the more predictable is energy expenditure. The grass substrate exhibited the greatest linearity between detection distance and capture time, though significant correlations were also exhibited by leaf litter and rock (Table 3). Bare ground demonstrated a very poor correlation between the two parameters.

SUBSTRATE ASSOCIATIONS

Since grass substrates provide *L. santrita* significantly greater prey capture efficiency than other substrates, one would expect this spider to exhibit a preference towards them. Testing for active choice, however, is a problem because wandering spiders do not occupy specific sites for any length of time: individual spiders are difficult to locate and to follow. Our observations of *L. santrita* in the field indicate this spider to be basically a sit-and-wait predator. Unlike members of the genus *Pardosa*, *L. santrita* does not frequently move up and down grass stems in search of prey. Rather movements by *L. santrita* result in changes in habitat position. Greenquist and Rovner (1976) avoided the problem by limiting their work on stratum choice of *Lycosa* and *Schizocosa* to artificial substrates in laboratory cages, though Edgar (1971) has studied the seasonal movements of (*Pardosa*) *lugubris* in the natural habitat. We attempted to study habitat choice in the field with natural populations.

Methods.—The association of *L. santrita* with specific substrates in the study area was determined through field censusing of spider activity. Five adjacent quadrats (30 m long and 1 m wide) were laid parallel to the creek bed. These were sampled at random with two

Table 3.—Correlation Coefficients Showing the Significance of Linear Relationships between Distance at Orientation and Capture Time for different substrates.

Substrate	r	Tabular r
Grass	0.9428	$r_{0.001(8)}=0.8721$
Rock	0.6836	$r_{0.05(8)}=0.6319$
Leaf Litter	0.6824	$r_{0.05(8)}=0.6319$
Bare Ground	0.6177	not significant

constraints: 1) that each quadrat was examined once a day and 2) that all quadrats were sampled once in a 5 day period at each of the following times: 0600, 0900, 1300, 1700 and 1900 hours. A census consisted of a one minute examination of each square meter of a quadrat for spider presence. Substrate type, location of the square meter within the quadrat, sex of the spider and activity at the time of observation were recorded for all sightings. These censuses were conducted over a 21 day period in August and September 1975.

The representation of different substrate types in the habitat was assessed through use of cover estimates made within the same quadrats used in the activity censuses. A gridded, plexiglass sheet was placed over each meter and the number of 20 x 20 cm squares occupied by each of the substrates (rock, bare ground, leaf litter and grass) was tallied.

Results.—While censusing spider activity, we found habitat associations to vary with time, coinciding with the maturation state of the spiders. For this reason, the analyses reported here were performed on subsamples consisting of individuals of similar age and sex.

Using the frequency representation of substrate cover scores as the expected, the association of spiders with specific substrates was tested for by application of chi square tests (Snedecor and Cochran 1967). Grass was found to be the only substrate with which the spiders exhibited significant associations. Penultimate spiders demonstrated the greatest positive association with this substrate (P - females: $X^2 = 20.6$, $P < 0.005$; P - males: $X^2 = 10.6$, $P < 0.005$); adult females exhibited less association ($X^2 = 7.0$, $P < 0.01$) and males exhibited the least significant association ($X^2 = 5.3$, $P < 0.025$). A look at the activity of the various age and sex classes of spiders on the substrates explains the decrease in association noted with age (Fig. 1). Mature females appear to utilize patches containing bare ground and rock to a greater extent than younger females, while adult males show greater activity in areas containing more bare ground and leaf litter. Differences in substrate association existing between younger spiders and adults are significant (P - female with Ad - female: $X^2 = 18.1$, $P < 0.005$; P - male with Ad - male: $X^2 = 19.6$, $P < 0.005$). No significant differences were found to exist between the habitat associations of penultimate females and those of penultimate males ($X^2 = 4.3$, $P > 0.30$).

Younger spiders primarily occupy the grass substrate associated with the woodland floor. On the other hand, adult spiders are located in the vicinity of the creek (Fig. 2). (A chi square test completed on the quadrat associations of spiders shows adult males and females to be more active in quadrats 1 and 2 and penultimate spiders in 4 and 5 ($X^2 = 8.8$ $P < 0.07$).

This movement toward the creek is further supported by our observations on the movements of marked individuals over an eighteen day period. In a significant number of sightings (Binomial Test, $N=85$, $P < 0.05$), individual spiders were moving towards the

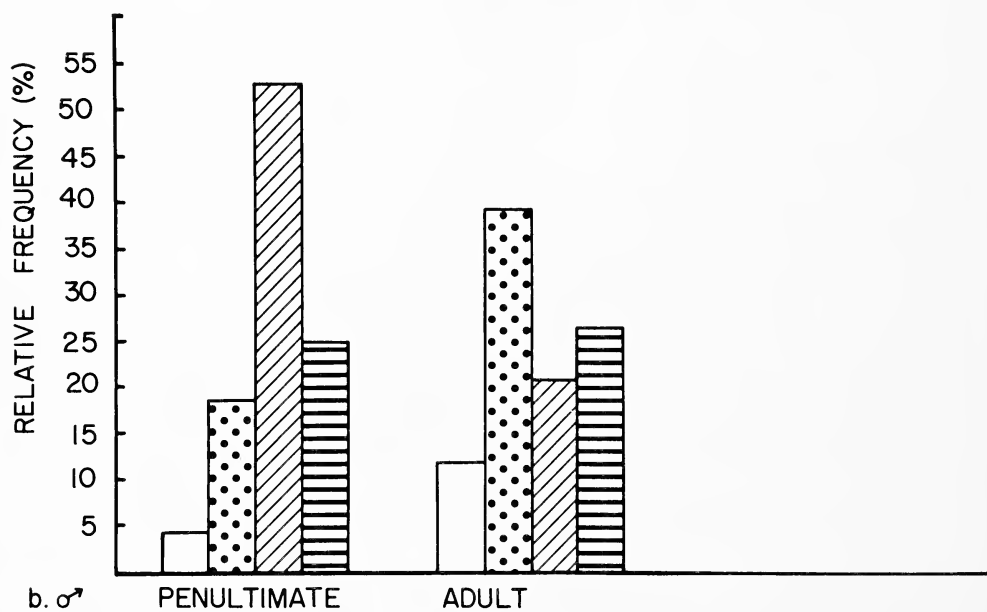
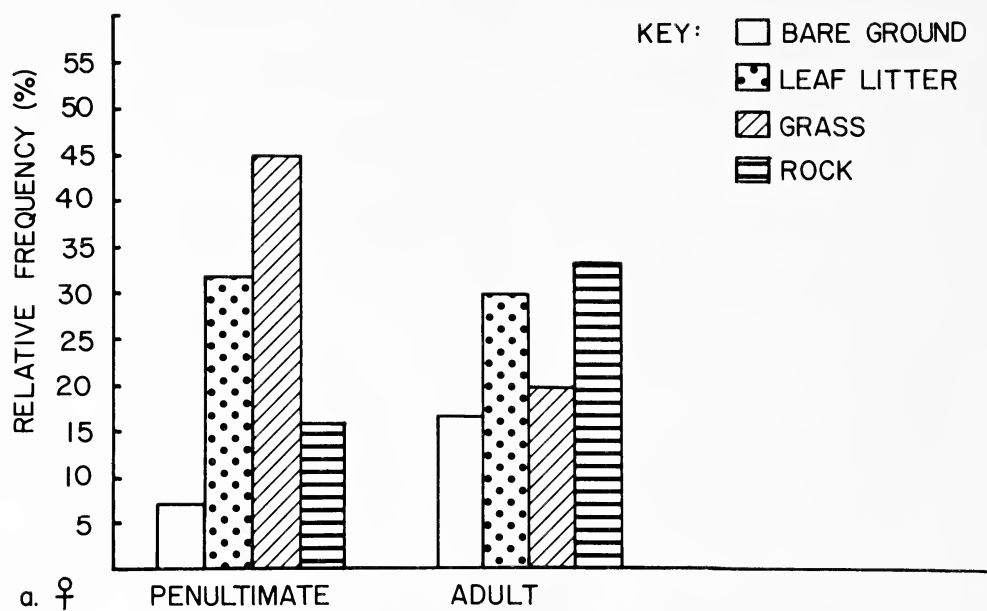


Fig. 1.—Relative frequency of spider associations with (narrow bar), and activity on (wide bar), different substrates: 1a, females; 1b, males.

creek as opposed to away from it. When we consider the additional facts that lycosids are highly mobile and that the distances involved in this study are well within the dispersal capabilities of wolf spiders (Uetz 1976), we must conclude that the results presented here indicate that *Lycosa santrita* is exhibiting active habitat selection.

PREY AVAILABILITY

Riechert (1976) has shown that spider species can detect areas of high prey density and move into them [the aggregational response of Readshaw (1973)]. It is possible that the changes in association with different habitat patches exhibited by *L. santrita* reflect changes in the local abundances of prey and associated moves by these spiders in search of new patches of high prey density. The following experiment was designed to test this hypothesis.

Methods.—Prey availability is herein defined as those prey coming within the detection range of the spider. Balls of chicken coop wire intermeshed with string and coated with a tree banding compound (Stikem Special^R) were used in its estimation. Each ball was 9

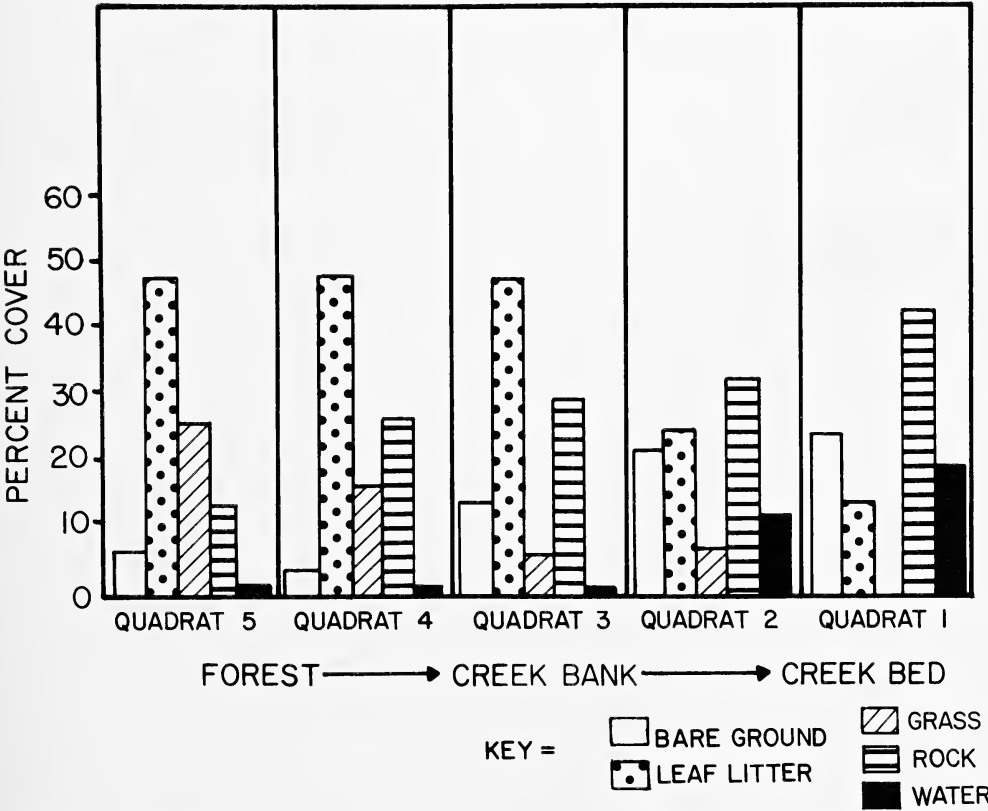


Fig. 2.—Absolute representation (% cover) of various substrates in riparian habitat. Position of sample quadrats relative to creek bed and forest indicated. Quadrats are 1 meter and extend 30 meters parallel to creek bed.

cm in diameter, assuming that the spider was located in the center and could detect prey within a radius of 4.5 cm. [This detection radius was determined through the offering of tethered prey at various distances to stationary spiders in the habitat (Kronk 1976)]. Three balls were placed on each of four substrate types and prey items were collected once every 24 hours for 21 days during August and September of 1975. (Sample adequacy was set as that N which provided a standard error of equal to or less than 10% of mean prey density). The number of prey caught on a ball during the collection period and the total dry weight of these prey were recorded for all samples.

Results.—Analyses of variance computed on the total dry weights and densities of prey associated with specific substrates showed a significant variation to exist (Table 4). The Duncan's multiple range test was then used to determine which substrates differed significantly from each other (Table 5). Prey availability was significantly greater on patches of bare ground than on other substrates. This is not unexpected as bare ground is prominent at the creek edge and insects seeking water can best obtain it from this type of substrate which tends to absorb moisture.

What is unexpected, however, is the observation that differences in prey availability associated with specific substrates were maintained throughout the study period—despite the changes in substrate association exhibited by the spiders during the same time period. This observation comes from comparisons made between the catches from a particular substrate during the first 10 days of the experiment with those from the last 10 days. A Cox and Stuart test for trend (1955) showed no significant differences in prey density or dry weight to exist on any of the substrates between the first half of the sampling period and the second half. Thus, changes in habitat association do not appear to be related to changes in insect abundance.

Table 4a.—Analysis of Variance for Dry Weight of Available Prey (DF = Degrees of Freedom, SS = Sum of Squares, MS = Mean Square).

Source of Variation	DF	SS	MS	F	Tabular F
Total	314	345961.14			
Treatments	4	108124.25	27031.06	11.21	$F_{0.005(4,80)}=4.07$
Replication	20	30522.47	1526.12	0.63	$F_{0.05(20,80)}=1.72$
Rep. X Trt.	80	192965.05	2412.06	35.30	$F_{0.005(80,210)}=1.47$
Error	210	14349.37	68.33		

Table 4b.—Analysis of Variance for Available Prey Density.

Source of Variation	DF	SS	MS	F	Tabular F
Total	314	32214.97			
Treatments	4	9334.24	2333.56	31.56	$F_{0.005(4,80)}=4.07$
Replication	20	5957.37	297.87	4.03	$F_{0.005(20,80)}=2.32$
Rep. X Trt.	80	5916.03	73.95	1.41	$F_{0.025(80,210)}=1.35$
E Error	210	11007.33	52.42		

Table 5.—Results of Multiple Range Tests: (a) for prey weight underlined area indicates values not significantly different from each other ($P > 0.05$). Prey weight is significantly less on rocks, litter, and grass than on bare ground, and less on grass than on rocks and litter; (b) available prey density is significantly different from other substrates on all substrates ($P < 0.05$).

a. For Prey Weight:

Statistic	Substrates			
	Bare Ground	Rock	Litter	Grass
Treatment \bar{X} (mg. dry wt.)	21.4	<u>9.7</u>	<u>8.2</u>	4.3

b. For Prey Density:

Statistic	Bare Ground	Rock	Litter	Grass
Treatment \bar{X} (number)	61.7	36.0	25.9	13.4

DISCUSSION

Numerous factors appear to be influencing *L. santrita*'s choice of habitat. These include capture efficiency, energy needs as they vary with age, prey availability, the availability of potential mates and protection from predation. The proposed relationship among these factors is shown in Table 6. Despite the fact that association with areas predominantly covered with grass affords less prey, penultimate spiders inhabit these areas. In doing so, this spider appears to be minimizing uncertain time investments in prey capture. (Grass substrates contain the greatest predictability of capture time for prey located at specific distances from the spider). This time and energy investment is less certain for other substrates wherein the degrees of follow-up search and pursuit required for specific prey at given distances vary markedly. Association with the grass substrate also affords *L. santrita* protection from potential predation by spider wasps (Pompilidae) which are numerically prominent in the study area and are known predators of *L. santrita* (unpublished observations).

The tendency to stay on grass substrates which afford maximum capture efficiency and protection from predation, appears to be overridden by the need of adult female spiders to maximize food intake for the reproductive effort. Females at this time move to the bare ground areas adjacent to the creek bed where prey densities are considerably higher. The necessity of this move is supported by the results of a separate feeding and weight gain experiment with *L. santrita*. Twenty-four penultimate female spiders were collected, weighed and placed in containers covered with cheese cloth. These individuals were fed at one of four feeding levels on alternate days for a three week period. (On non-feeding days, the containers were placed in the study area, exposing the captives to temperatures and humidities experienced under natural conditions). On the final day of

Table 6.—Significance of habitat choice to spiders of different age and sex.

	Juveniles	Adult Females	Adult Males
General Substrate Association	Grass	1) Bare ground	1) Leaf Litter
Location in Habitat	Forest Floor	2) Rock	2) Bare Ground
Property Maximized	Capture Efficiency	Prey Availability	Mating Probability
Property Minimized	Potential Predation		Potential Predation

the experiment, the captives were weighed again, along with 10 newly captured spiders. The prey consumption required for specific weight gains was calculated from the resulting data (Table 7). The dry weight of prey required to realize the weight gain observed in the field at the transition period between the penultimate and adult stage was estimated to be 3.51 mg/day. This weight is available on the grass substrates (Table 5). However, in the experiment we find that the spiders are capable of consuming weights of prey of 17.56 mg/day. These quantities of prey are only available on bare ground substrates in the study area (Table 5).

Grasses, though less prominent in the creek bed are still used by females, when possible, in prey capture. Females also use the rock substrate in the creek area where prey availability is higher than on the grass or adjacent litter substrates though less than on the bare ground (Table 5). Rock affords significantly greater capture efficiency than bare ground (Table 3), and spiders in the vicinity of the creek may prefer it to the bare ground for this reason.

Adult males are known to be erratic in their food consumption (Riechert 1978). It appears unlikely, then, that their move to the creek bed area is related to food needs. Male spiders are most active in the leaf litter adjacent to bare ground and rock patches being utilized by females. They can best avoid predators in this habitat, while their close proximity to the females ensures a chance at mating. (We assume that females also seek shelter in the leaf litter during periods of inactivity).

Additional benefits to the population may result from the habitat selection of adult *L. santrita*. For example, it may minimize competition with juveniles for prey and/or minimize cannibalism of juveniles by adults.

The mechanisms by which these changes in substrate associations might be achieved are known from studies with other spiders. Riechert (1976), for instance, has shown that spiders search for and settle in areas of high prey density. In addition, Edgar (1971) in a study of *L. (Pardosa) lugubris* found that the adults moved to areas of high prey availability and away from areas occupied by younger spiders. *Lycosa santrita* can use the sensory capabilities of its tarsal slit organs to similarly locate areas of abundant prey. The increased hunger levels experienced by the females might provide the stimulus needed to migrate. The move by males to the vicinity of the creek is probably not mediated by prey activity. Rather, males in search of potential mates may follow the dragline silk laid down by females as they move into the creek bank area: experiments completed by Tietjen (1977) show that a pheromone is laid down with the dragline silk of female lycosids and that males actively follow these pheromone trails. Tietjen's (1977) study and a study conducted by Dondale and Hedgekar (1973) suggest that moisture on the bare ground substrate would inactivate the pheromone. Therefore, the pheromonal attraction would be expected to be the greatest on the dry litter located on the creek bank.

Table 7.—Summary of Female *Lycosa santrita* Feeding Dynamics [*Estimates calculated from laboratory results with weight gain in the field setting scale].

Feeding Characteristics	Laboratory Groups (wet wt.)				Field (wet wt.)	Field Equivalent (dry. wt)
\bar{X} mg consumed/day	36.67	20.00	15.00	10.17	7.17*	
\bar{X} mg gained/day	8.33	6.75	3.17	2.20	1.79	
\bar{X} mg prey available/day	99.63	50.95	26.22	13.58	9.81*	3.51
Assimilation Coefficient (mg gained/mg consumed)	.23	.31	.23	.25		
Ingestion Coefficient (mg consumed/mg available)	.66	.72	.73	.74		
Mg prey available/day to optimize consumption					49.32*	17.56

The system of habitat choice described herein is an example of a complex life history in which the particular "strategy" used at a given time changes with age and differs with the sex of the individual. The view the researcher receives at any point in time thus merely reflects the resulting compromise of the many needs and selection pressures impinging upon the individual spider at that time and earlier times in its life cycle. Understanding of the "suite" of adaptations involved in the overall selection strategy requires continued study throughout the life cycle of the species population.

Confusion also exists concerning the relative importance of various components to the life history strategy. Recent studies emphasize such parameters as clutch size, degree of parental investment, longevity etc. (Wilbur et al. 1974, Pianka 1976). Our work suggests that complexities involved in habitat choice are just as important to optimal reproductive success as these other aspects of life histories. Stearns (1977) in his review of the subject concurs.

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BOOK REVIEW

WEBERKNECHTE, OPILIONES. Vol. 64 in *Die Tierwelt Deutschlands*. Gustav Fischer, Jena. 464 pp., 815 figs. 1978.

The publication of this important volume is a benchmark in the history of our knowledge of the Opiliones, that little-studied (and consequently poorly understood) order of Arachnida. Among previously published works of similar ambition, only Bishop's brief "Phalangida of New York" and Šilhavý's volume in *Fauna ČSR* compare favorably. Central Europe has become, at this one stroke, the best-known region in the world as regards its opilionid fauna. Martens draws heavily on his own work and that of his colleagues Šilhavý, Gruber, Ausobsky, Staręga, Thaler, and others, to bring together practically all that is known about the Central European opilionid fauna. In even a comparatively well-collected region as the Northeastern United States, new species and genera are still being found, perhaps suggesting how long it will be before something similar to Martens' book can be prepared for North America.

Comparison may be invited with Roewer's 1923 book, "Die Weberknechte der Erde," but none can be made. Roewer's volume was merely a compendium from the literature of all names published in Opiliones as of 1923; Roewer frequently did not examine material of the species he discussed, included virtually no ecological, behavioral or physiological information, and was an inveterate "splitter," resulting in the Opiliones being held up by Mayr (1969) as an example of an exceptionally fractionated group, with 1700 species in 500 genera, more than 300 of which were monotypic. Indeed, Roewer sometimes placed males and females of the same species in different genera. Thus, despite its attempt at scope, his treatise is of limited value and serves mainly as a guide to the older literature.

Martens' book, however, includes available ecological and behavioral information for each species discussed, in addition to an introductory chapter dealing with such considerations for the order as a whole. By narrowing his focus geographically, Martens is able to deal much more deeply with each species he treats.

The illustrations (which are profuse) are excellently executed, but the printing process typical of *Tierwelt*, together with the inexpensive grade of paper used, has resulted in the fine detail of some of them being obscured or even lost (see especially figs. 403-405 and figs. 284 and 287). Too great a degree of reduction in drawings already quite dark (figs. 158, 166, 173, etc.) has made them virtually solid black. This is unfortunate, but since these illustrations are in some cases the only ones available, their publication is welcome.

A number of nomenclatorial questions also arise. There is a repeated (p. 54, 186, 187) casual mention of a monotypic family Crosbyidae for the North American *Crosbycus*. It is difficult to know whether or not this constitutes a valid proposal for such a family. Martens also recognizes Sabaconidae as a separate family, but does not deal with the position of *Tomicomerus*.

On the other hand, his clear exposition of the Family Phalangiidae greatly improves our understanding of this group. This is a real trouble spot in opilionid taxonomy. Martens for the first time lays out the issues; it is very difficult to distinguish between Leiobuninae, Gyantinae and Gagrellinae as presently constituted. Similarly, in the subfamily Oligolophinae, the generic complex *Oligolophus*–*Paroligolophus* presents difficulties, as does the complex *Odiellus*–*Lacinius*.

From the standpoint of the American opilionologist, this work will be invaluable for two reasons. First, a number of the genera found in North America of which we have an

incomplete understanding have as their types European forms; Martens presents detailed descriptions and good illustrations of some of these. Secondly, numerous European species are being discovered (even in recent years; see Muchmore, 1963; Bell, 1974; Bragg and Holmberg, 1975) as introduced to the United States and Canada; with Martens' book on hand, we can avoid falling into the error of thinking these new.

In summary, this volume may be heartily recommended for inclusion in the library of every serious arachnologist.

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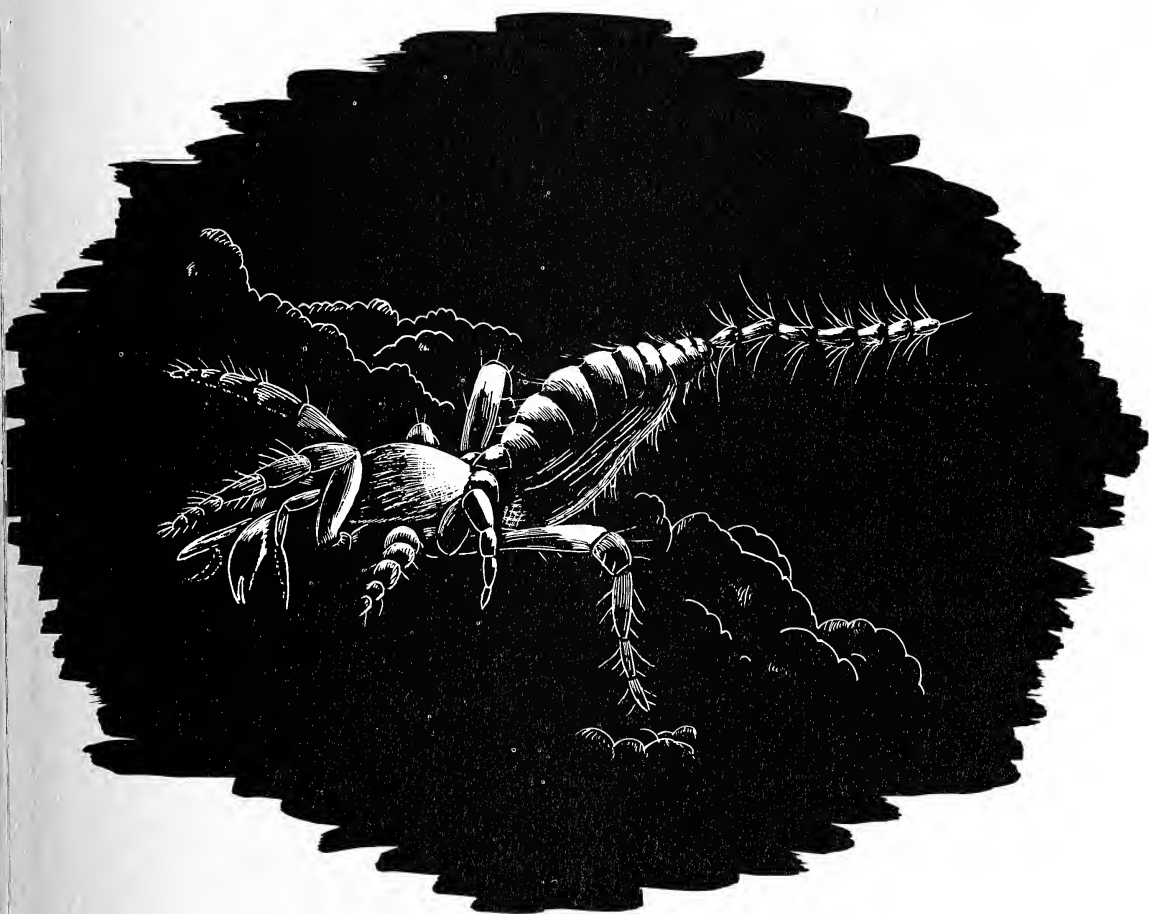
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REVISION DEL GENERO *EUSTIROMASTIX* SIMON, 1902 (ARANEAE, SALTICIDAE)

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ABSTRACT

The study of the type specimens of the species of *Eustiromastix* as well as from some large collections of undetermined material, has allowed us to establish the following new combinations and synonymies: *Eustiromastix rufohirtus* Simon, 1902 = *Freya rufohirta* (Simon, 1902) n.comb.; *Evophrys keyserlingi* Taczanowski, 1879 = *Eustiromastix keyserlingi* (Taczanowski, 1879) n.comb.; *E. styliferus* Simon, 1902 = *E. major* Simon, 1902; *Theratoscirtus affinis* Caporiacco, 1954 = *E. major* Simon, 1902; *E. obscurus* Mello-Leitão, 1942 [non *E. obscurus* (Peckham & Peckham, 1893)] = *E. parobscurus* Roewer, 1951 = *E. pantherinus* Mello-Leitão, 1942. The name *Eustiromastix obscurus* Mello-Leitão, 1942 is a primary homonym of *E. obscurus* (Peckham & Peckham, 1893), type species of the genus. The species was given the new name *E. parobscurus* Roewer, 1951. In the present paper we establish that *E. obscurus* Mello-Leitão, 1942 and *E. pantherinus* Mello-Leitão, 1942 are synonyms, so the taxon has three synonyms. The name *E. obscurus* Mello-Leitão, 1942 must be rejected because it is a primary homonym and we adopted for the species the name *E. pantherinus* Mello-Leitão, 1942 which is an available synonym older than *E. parobscurus* Roewer, 1951. *E. pantherinus* Mello-Leitão, 1942 is not an *Eustiromastix* species and will be transferred to another genus, now under study.

E. guianae Caporiacco, 1954 and *E. chaperi* Simon, 1902, are considered *species inquirenda* because the type specimens are lost and the original descriptions are imperfect. Some confusion seems to have occurred with the drawing of the palp of *E. chaperi* by E. Simon.

E. obscurus (Peckham & Peckham, 1893), *E. vincenti* (Peckham & Peckham, 1893) and *E. moraballi* Mello-Leitão, 1940 are redescribed. The characteristics of the female of *E. major* Simon, 1902, are given for the first time. Three new species are described: *E. bahiensis* n.sp. and *E. macropalpus* n.sp. from Brazil and *E. intermedius* n.sp. from Venezuela.

RESUMEN

El estudio de los ejemplares típicos de las especies de *Eustiromastix* así como de abundantes colecciones de material indeterminado, ha permitido establecer las siguientes nuevas combinaciones y sinonimias: *Eustiromastix rufohirtus* Simon, 1902 = *Freya rufohirta* (Simon, 1902) n.comb.; *Evophrys keyserlingi* Taczanowski, 1879 = *Eustiromastix keyserlingi* (Taczanowski, 1879) n.comb.; *E. styliferus* Simon, 1902 = *E. major* Simon, 1902; *Theratoscirtus affinis* Caporiacco, 1954 = *E. major* Simon 1902; *E. obscurus* Mello-Leitão, 1942 [no *E. obscurus* (Peckham y Peckham, 1893)] = *E. parobscurus* Roewer, 1951 = *E. pantherinus* Mello-Leitão, 1942. El nombre *Eustiromastix obscurus* Mello-Leitão, 1942 es un homónimo primario de *E. obscurus* (Peckham y Peckham, 1893), especie tipo del género. La especie recibió el nuevo nombre de *E. parobscurus* Roewer, 1951. En la presente publicación se establece que *E. obscurus* Mello-Leitão 1942 y *E. pantherinus* Mello-Leitão 1942 son sinónimos, por lo cual el taxon tiene tres nombres sinónimos. Se adopta para la especie el nombre de *E. pantherinus*

¹Miembro del Consejo Nacional de Investigaciones Científicas y Técnicas. Buenos Aires.

Mello-Leitão, 1942 que es un sinónimo utilizable, más antiguo que el de *E. parobscurus* Roewer 1951. *E. pantherinus* Mello-Leitão, 1942 no es *Eustiromastix* y será transferida a otro género, actualmente en estudio.

E. guianae Caporiacco, 1954 y *E. chaperi* Simon, 1902 se consideran *species inquirenda* porque los tipos se han perdido y las descripciones originales son imperfectas. Parece haber existido alguna confusión por parte de E. Simon con el dibujo del palpo de *E. chaperi*.

E. obscurus (Peckham y Peckham, 1893), *E. vincenti* (Peckham y Peckham, 1893) y *E. moraballi* Mello-Leitão, 1940 se redescubren. Se dan por primera vez los caracteres de la hembra de *E. major* Simon, 1902. Se describen tres nuevas especies: *E. bahiensis* n.sp. y *E. macropalpus* n.sp. de Brasil y *E. intermedius* n.sp. de Venezuela.

INTRODUCCION

Eustiromastix Simon, 1902, al igual que otros géneros de los grupos *Hylleae* y *Plexippeae* (sensu Simon, 1903) son difíciles de diferenciar. Algunas de las especies que en esta contribución se consideran como *Eustiromastix*, han sido descriptas como *Evophrys* y *Theratoscirtus*; otras, que ahora se excluyen, se transfieren a otros géneros, como *Freya*.

La separación entre *Freya* y *Eustiromastix*, indudablemente muy próximos, debe hacerse por la diferente estructura del aparato copulador. *Freya* se caracteriza por un palpo corto y grueso, con apófisis tibiales a menudo convertidas en tubérculos y el estilo macizo y robusto. *Eustiromastix* tiene largos tarsos, a veces doblados en ángulo en la mitad apical y estilo filiforme, larguísimo.

En las formas más características [*E. obscurus*, (Peckham y Peckham, 1893), *E. macropalpus* sp.n.] el bulbo es disciforme y el estilo describe varias vueltas a su alrededor. Correspondiendo a esta estructura del aparato masculino, las hembras tienen los conductos de las espermatecas largos, membranosos, plegados, ovillados o en espiral.

Otro grupo de especies [*E. vincenti* (Peckham y Peckham, 1893), *E. moraballi* Mello-Leitão, 1940, *E. bahiensis* sp.n.] tiene el bulbo alargado y el estilo, si bien es largo y filiforme, no circunscribe al bulbo. A estas formas corresponden también conductos de las espermatecas ovillados o espiralados.

La semejanza en el aspecto general, quetotaxia y coloración entre las especies es grande. *E. major* y *E. bahiensis* sp.n. han sido colectadas juntas en el Estado de Bahía, Brasil, en cantidades relativamente abundantes. Las hembras de estas dos especies se distinguen solo por los epiginos, ya que el color difiere nada más que por algunas manchas de pelos. Los machos de *E. bahiensis* sp.n. se ubican, por la estructura de los palpos, en un grupo diferente de los de *E. major*.

Finalmente, *E. intermedius* sp.n. presenta un bulbo disciforme como *E. obscurus* y estilo de posición prolateral como en *E. vincenti*, por lo que es una especie que vincula los dos grupos mencionados anteriormente. Cuando se encuentre la hembra de esta última especie, se dispondrá de más caracteres para confirmar o corregir su ubicación en el género, un tanto dudosa.

METODOS

Las medidas se expresan en milímetros, con fracciones hasta milésimos. Se han tomado según métodos indicados en publicaciones anteriores (Galiano 1963).

ABREVIATURAS.—O.M.A., ojos medios anteriores; O.L.A., ojos laterales anteriores; O.L.P., ojos laterales posteriores; p, prolateral; r, retrolateral; v, ventral; d, dorsal; ap,

apical; M.A.C.N., Museo Argentino de Ciencias Naturales "Bernardino Rivadavia;" B.M.N.H., British Museum (Natural History); M.N.H.N., Muséum National d'Histoire Naturelle, Paris; M.N.R.J., Museu Nacional de Rio de Janeiro; M.L.P., Museo de La Plata; M.C.Z., Museum of Comparative Zoology, Harvard; I.Z.A.P.S., Institute Zoologique de l'Académie Polonaise des Sciences; C.E.P.E.C., Comissao Executiva do Plano de Recuperacao Economico Rural da Lavoura Cacaueira; M.E.G., Colección María Elena Galiano.

Género *Eustiromastix* Simon, 1902

Cybele Peckham y Peckham 1893:695 (n. gen.) (praeocup); Petrunkevitch 1928:216 (*Eustiromastix*).
Theratoscirtus Caporiacco 1954:174.

Euophrys (part) Taczanowski 1879:285.

Eustiromastix Simon 1902:416 (nom. nov. pro *Cybele*), 1903:724, 730, 733, 740; Petrunkevitch 1928:198; Bonnet 1956:1843.

Diagnosis.—Difiere de *Freya* por presentar el tarso del palpo alargado, a veces doblado en la mitad apical, formando un ángulo y el estilo muy largo y filiforme. En *Freya* el tarso es corto y grueso y el estilo breve y robusto. Conductos de las espermatecas membranosos, largos, plegados, ovillados o espiralados.

Descripción.—Prosoma moderadamente alto (alto/largo = 50-62), con profunda estría torácica. Area ocular ocupa aproximadamente la mitad del largo del prosoma (largo área ocular/largo prosoma = 43-55); más ancha adelante que atrás (raramente paralela) y más ancha que larga (largo/ancho = 62-74). Fila anterior de ojos recurva por los bordes superiores; ojos laterales anteriores mayores que el radio de los medios. Ojos de la 2a. hilera por lo común más cerca de O.L.P. Clípeo menor que el radio de O.M.A. Láminas maxilares sin apófisis o mucrones. Borde anterior del esternón del mismo ancho que la base del labio. Quelíceros verticales; con dos dientes en promargen del surco ungueal y uno en retromargen. Longitud relativa de las patas del macho I-IV-III-II y de la hembra IV-III-I-II. Hay dos excepciones a esta fórmula: *E. macropalpus* sp.n., III-IV-I-II en ambos sexos y *E. intermedius* sp.n. con pata I más corta que la IV. Pata III en todas las especies con fémur, patella y tibia más gruesos que los de pata IV. Tibia y metatarso de pata III más cortos que los de IV; patella III siempre mayor que IV. Longitud de tibia más patella III en las formas típicas (*E. obscurus*, *E. macropalpus* sp.n., *E. major*) mayor que tibia más patella IV; en otras especies menor. Espinas numerosas y fuertes. I: fémur d l-l-l, p l ó 2, r l (ap); patella p 0 ó 1; tibia v 2-2-2, p l-l ó l-l-l; metatarso v 2-2. II: fémur d l-l-l, p l ó 2, r l ó 2 (ap), a veces p l y r l, medianas; patella p l; tibia v 2-2-2, p l-l ó l-l-l; metatarso v 2-2, a veces p l ap. III: fémur d l-l-l, p l ó 2, r l ó 2 (ap), a veces p l y r l, medianas; patella p l, r l; tibia v lp-2; p l-l-l, r l-l-l, a veces d l; metatarso v 2-2, p l-2, r l-l-2. IV: fémur d l-l-l, p l ó 2, r l (ap), a veces p l y r l, medianas; patella p l, r l; tibia v lp-2, p l-l-l, r l-l-l, a veces d l; metatarso v 2-2, p l-l-2, r l-l-2. Hembras con igual quetotaxia que machos, a veces p l en tibia I. Pata I del macho con pelos pardos largos, delgados, más abundantes en cara inferior de tibia y metatarso; no forman fimbrias. Palpo del macho grande en relación al cuerpo; con una apófisis retrolateral mediocre; tarso muy grande, a menudo doblado hacia la cara retrolateral o hacia la inferior (*E. obscurus*, *E. macropalpus* sp.n., *E. moraballi*, *E. bahiensis* sp.n.). Bulbo disciforme; estilo muy largo y filiforme, circunda al bulbo describiendo una o más vueltas (*E. obscurus*, *E. major*, *E. macropalpus* sp.n.). En un grupo de especies alejado de las formas típicas, el bulbo es alargado y protuberante; el estilo largo y curvo no lo circunda (*E. vincenti*, *E. moraballi*, *E. bahiensis* sp.n.). Aparato

genital femenino con entradas de los conductos pequeñas y circulares. Conductos membranosos, largos, plegados, ovillados o espiralados. Color general pardo, con una banda amarillenta longitudinal, desde la región torácica al extremo apical del opistosoma. Prosoma a menudo con bandas blancas laterales y clípeo con barbas blancas. Pata I del macho oscura; restantes pares pardo claro o amarillo, con manchas o anillos negruzcos en articulaciones. Hembra con pata I pardo claro.

Especie tipo.—*Cybele obscura* Peckham y Peckham, 1893.

Eustiromastix obscurus (Peckham y Peckham, 1893)
(Figs. 1-3, 24)

Cybele obscura Peckham y Peckham 1893:695, t. 61 figs. 3-3c (macho y hembra sp.n.).

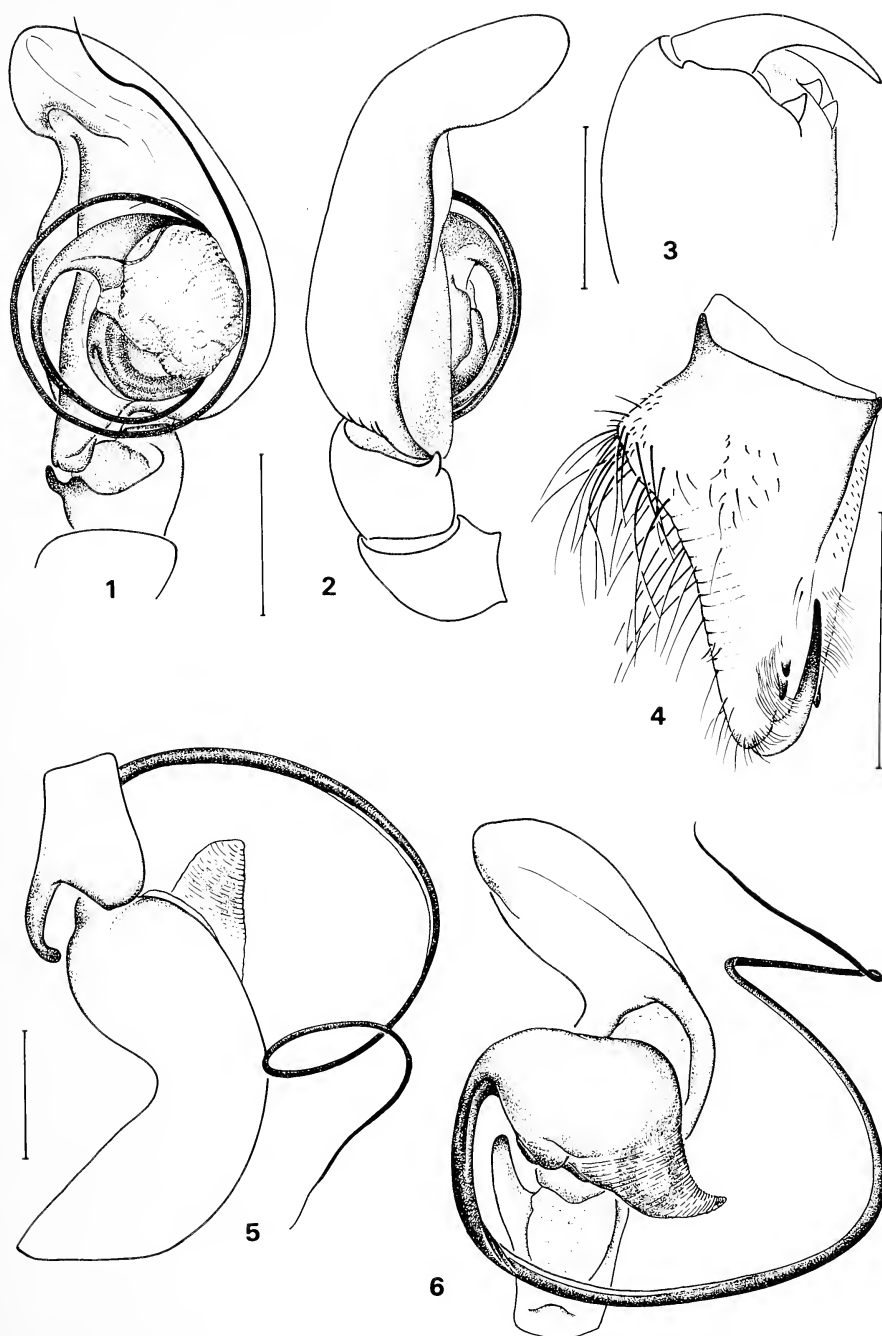
Eustiromastix obscurus: Simon 1903:730, 740; Petrunkevitch 1911:650, 1928:198; Roewer 1954:1079; Bonnet 1956:1843.

Redescripción del Lectotypus macho.—Largo total 5,800. Prosoma: largo 2,766; ancho 2,000; alto 1,366. Clípeo: alto 0,166. Área ocular: largo 1,200. Ancho de la hilera anterior 1,933; de la posterior 1,833. Ojos de la 2a. hilera, separados de O.L.A. por 0,300 y de O.L.P. por 0,200. Diámetro de O.M.A. 0,600. Quelíceros: promargen grueso, elevado, sobrepasando la altura de los dientes promarginales. Patas: longitud relativa y espinas como en el género. Patella I con p 1 y tibia I con p 1-l. Tibia III con d 1 basal. Palpos: extremo del tarso doblado hacia la cara ventral; cara retrolateral con una depresión alargada. Bulbo disciforme, rodeado por el estilo filiforme que describe una vuelta y media a su alrededor (Figs. 1, 2). Opistosoma: largo 3,166.

Aspecto y color en alcohol.—Prosoma con suave declive torácico; color pardo anaranjado; región cefálica con pelos rojizos, orientados hacia adelante y hacia el medio. Bajo los O.L.A., una mancha de pelos blancos; clípeo glabro. Región torácica cubierta por pelos pardo oscuro y con banda longitudinal media, amarilla con pelos blancos. En cada costado, dos o tres banditas horizontales, submarginales, de pelos blancos. Quelíceros y láminas anaranjados. Esternón amarillo. Opistosoma pardo, con una ancha banda longitudinal amarilla, que tiene dos dilataciones: una subapical y otra mediana. Bordeando la base del opistosoma y siguiendo por los costados, una banda de pelos blancos. De cada lado, apicalmente, dos o tres manchitas amarillas con pelos blancos. En la base del opistosoma, a cada lado del pedicelo, un mechón de pelos blancos, erectos; entre ambos y por fuera de cada uno de ellos, pelos pardos, gruesos y erectos. Vientre amarillo, con algunas manchitas pardas. Pata I y II con fémur pardo; patella con la mitad basal amarilla y la apical parda; tibia y metatarso pardos con la parte media amarilla; tarso amarillo. Patas III y IV con una mancha mediana amarilla en el fémur; el resto como pata I. Sobre las manchas amarillas hay pelos blancos.

Localidad típica.—West Indies: St. Vincent, Seeward.

Material estudiado.—Lote típico formado por 2 machos y 1 juvenil de los cuales se designa el Lectotypus (B.M.N.H.). Lote rotulado "*Cybele vincenti*," de St. Vincent, con 13 juveniles y 6 hembras (B.M.N.H.). Estos ejemplares no son *E. vincenti*, pues el epigino y las espermatecas tienen una estructura diferente (Fig. 24). Parece posible que se trate de *E. obscurus*.



Figs. 1-3.—*Eustiromastix obscurus*, Holotypus macho: 1, palpo, ventral; 2, palpo, retrolateral; 3, quelícero, cara inferior.

Figs. 4-6.—*E. bahiensis* sp.n., Holotypus macho: 4, quelícero derecho, cara interna; 5, palpo, dorsal; 6, palpo, ventral (Escala 0,5 mm).

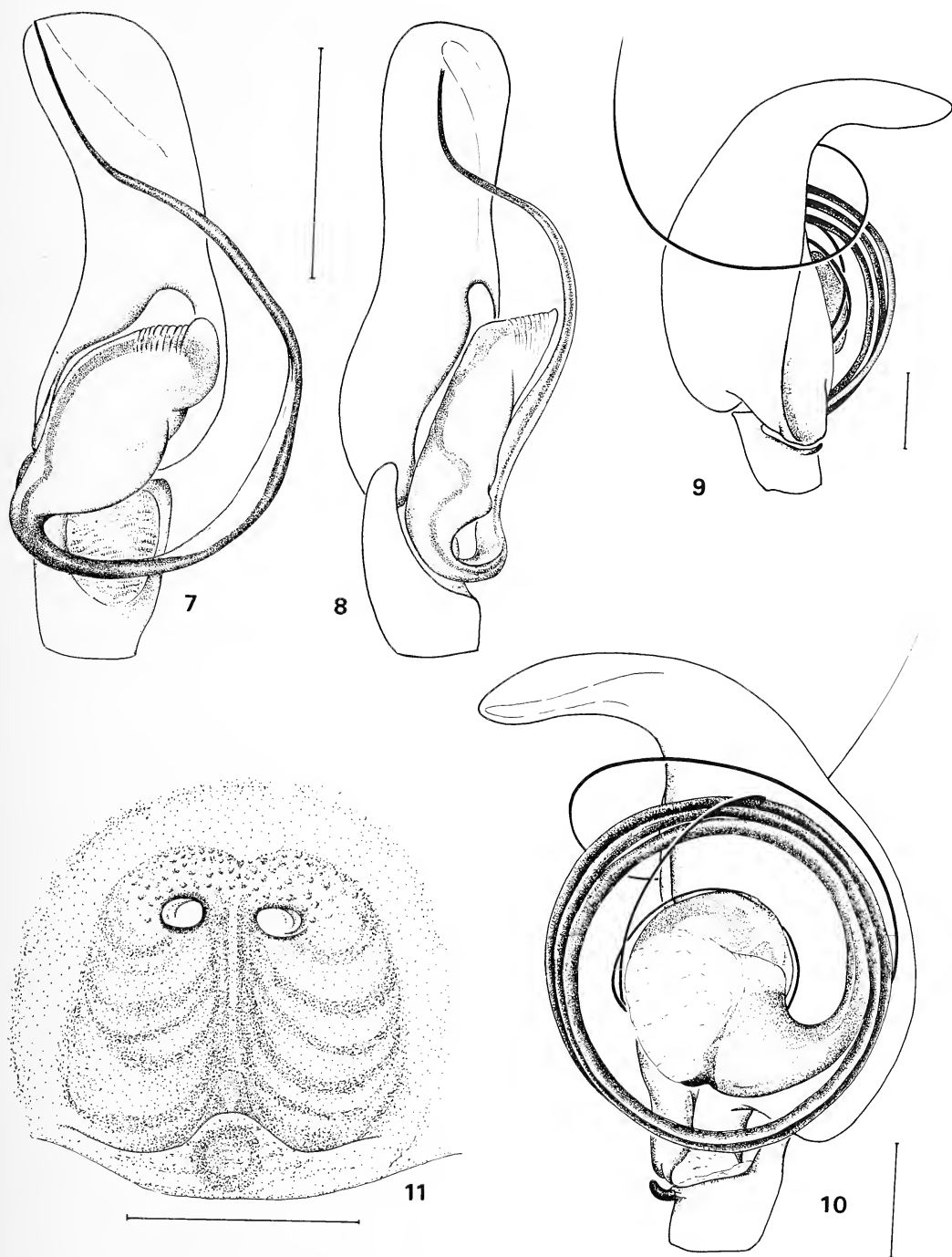
Eustiromastix major Simon, 1902
(Figs. 12, 13)

Eustiromastix major Simon 1902:416 (macho sp.n.), 1903:716, 725, 730 (no fig. 861 I); Petrunkevitch 1911:650; Roewer 1954:1079; Bonnet 1956:1843; Galiano 1963:348, t. 18 figs. 12, 13. (redescrpción).
Eustiromastix styliferus Simon 1902:418 (macho sp.n., *stylifera*), 1903:716, 725, 730, fig. 858 (*stylifer*); Petrunkevitch 1911:650 (*styliferus*); Roewer 1954:1079; Bonnet 1956:1843 (*stylifer*); Galiano 1963:350, t. 18 figs. 9, 10. *NUEVA SINONIMIA*.
Theratoscirtus affinis Caporiacco 1954:174, figs. 64, 64 a-b (macho sp.n.) *NUEVA SINONIMIA*.

Descripción dela Hembra Nº 7117 MACN.—Largo total 8,645. Prosoma: largo 3,666; ancho 2,933; alto 1,866. Clípeo: alto 0,166. Area ocular: largo 1,733. Ancho de la hilera anterior 2,633; de la posterior 2,566. Ojos de la 2a. hilera, separados de O.L.A. por 0,466 y de O.L.P. por 0,400. Diámetro de O.M.A. 0,800. Quelíceros: como en el género. Patas: longitud relativa y espinas como en el género. Patella I sin prolaterales; tibia I con p l. Opistosoma: largo 4,200. Epigino: Figs. 12, 13.

Aspecto y color en alcohol.—Prosoma pardo anaranjado; región cefálica más oscura con una ancha banda longitudinal media, amarilla con pelos blancos, desde el borde posterior del prosoma hasta el extremo anterior de la estría torácica y desde allí una delgada línea de pelos blancos hasta la altura de los ojos pequeños de la 2a. hilera. De cada lado del prosoma, una ancha banda submarginal amarilla cubierta por pelos blancos con borde superior ondulado; en el espacio bajo O.L.A. se divide en tres fajas de pelos blancos, horizontales, separadas entre si por pelos pardos. La banda mediana se continúa formando una densa barba blanca en el clípeo. Región cefálica cubierta por finos pelos pardos, algo rojizos; margen anterior con una banda transversa de pelos blancos que se extiende entre los bordes internos de los O.L.A. Detrás de los ojos de la 2a. hilera, un mechoncito de pelos blancos. Región torácica y margen del prosoma, con pelos pardo oscuro. Dorso del opistosoma pardo amarillento, cubierto por mechoncitos de pelos pardos y amarillos, formando un diseño atigrado. Una ancha banda longitudinal amarilla cubierta por pelos blanco amarillento, que se amplía en la mitad y apicalmente está cortada por 3 ó 4 bandas transversas de pelos pardos, con forma de acento circunflejo. En su parte basal, la banda incluye algunos pares de manchitas pardas. Bordeando la base y siguiendo por los costados hasta la mitad del opistosoma, una banda amarilla con pelos blancos. Costados del opistosoma con pelos pardos y manchas alargadas de pelos amarillentos. Vientre amarillento con lunares pardo oscuro; una mancha grande en el ápice. Pata I con fémur amarillo con tercio apical pardo; patella parda con mancha dorsal amarilla; tibia amarilla con anillo pardo basal y otro apical y banda parda retrolateral; metatarso amarillo con anillo angosto basal y otro más ancho, apical. Pata II como pata I, pero además con dos manchitas prolaterales en fémur. Pata III amarilla, con las siguientes manchas pardas: un anillo sub- basal y otro subapical en fémur; anillo basal y apical en patella; tibia con angosto anillo basal y otro, más ancho, apical; metatarso algo oscurecido hacia el ápice. Pata IV como pata III, pero con anillos basales y apicales en metatarso. Palpos con fémur y patella amarillos; tibia y tarso, pardos. En dorso de patella, tibia y tarso, manchas pardas. En patella y tarso, largos pelos pardos, prolaterales.

Macho Nº 7117 MACN.—Color en alcohol— Prosoma pardo oscuro, algo anaranjado, con pelos blancos, así: una gran mancha mediana trapezoidal, con base en extremo anterior de la estría torácica y ápice, romo, en la parte media del declive torácico. Otra mancha en mitad anterior de región cefálica, con borde anterior más angosto que su parte media; extremo posterior, ligeramente puntiagudo, a la altura del borde posterior de los



Figs. 7, 8.—*Eustiromastix vincenti*, Lectotypus macho: 7, palpo ventral; 8, palpo, retrolateral.
 Figs. 9-11.—*E. macropalpus* sp.n., Holotypus macho: 9, palpo, retrolateral; 10, palpo, ventral.
 Paratypus hembra: 11, epigino (Escala 0,5 mm).

relativa y espinas como en el género. Patella I con p l y tibia I con p l-l. Epigino: Fig. 25.

Aspecto y color en alcohol.—Prosoma pardo rojizo; banda media amarilla con pelos blancos en el declive torácico. Algunos pelos blancos en el margen del clípeo, pero sin barba. Lados del prosoma, con manchas pardo claro con pelos blancos, que no forman banda definida. Opistosoma pardo claro con manchas amarillas, que aumentan en los costados y en el vientre. Línea media dorsal con ancha banda amarilla, ampliada en su parte media. Patas amarillas con manchas y anillos pardos. Pata I y II con un anillo apical en fémur, patella, tibia y metatarso y un anillo basal en la tibia. Patas III y IV con anillos basales y apicales en fémur, tibia y metatarso; las patellas totalmente amarillas. Palpos pardo claro con manchas pardas en el ápice dorsal del fémur, dorso de patella y tibia y base del tarso.

Observación.—Los dos ejemplares del lote típico tienen el opistosoma arrugado por lo que no puede medirse. También está depilado y la coloración es borrosa. La estructura del aparato genital así como la quetotaxia y la proporción en las medidas de las patas permiten reconocer a esta especie como *Eustiromastix* por lo que se establece una nueva combinación.

Localidad típica.—Perú: Amable María.

Material estudiado.—Lote típico formado por 2 hembras, de las cuales se elige el Lectotypus. Col. Jelski 1871-1878, Nº 85 (I.Z.A.P.S.).

Eustiromastix vincenti (Peckham y Peckham, 1893)
(Figs. 7, 8, 14, 15)

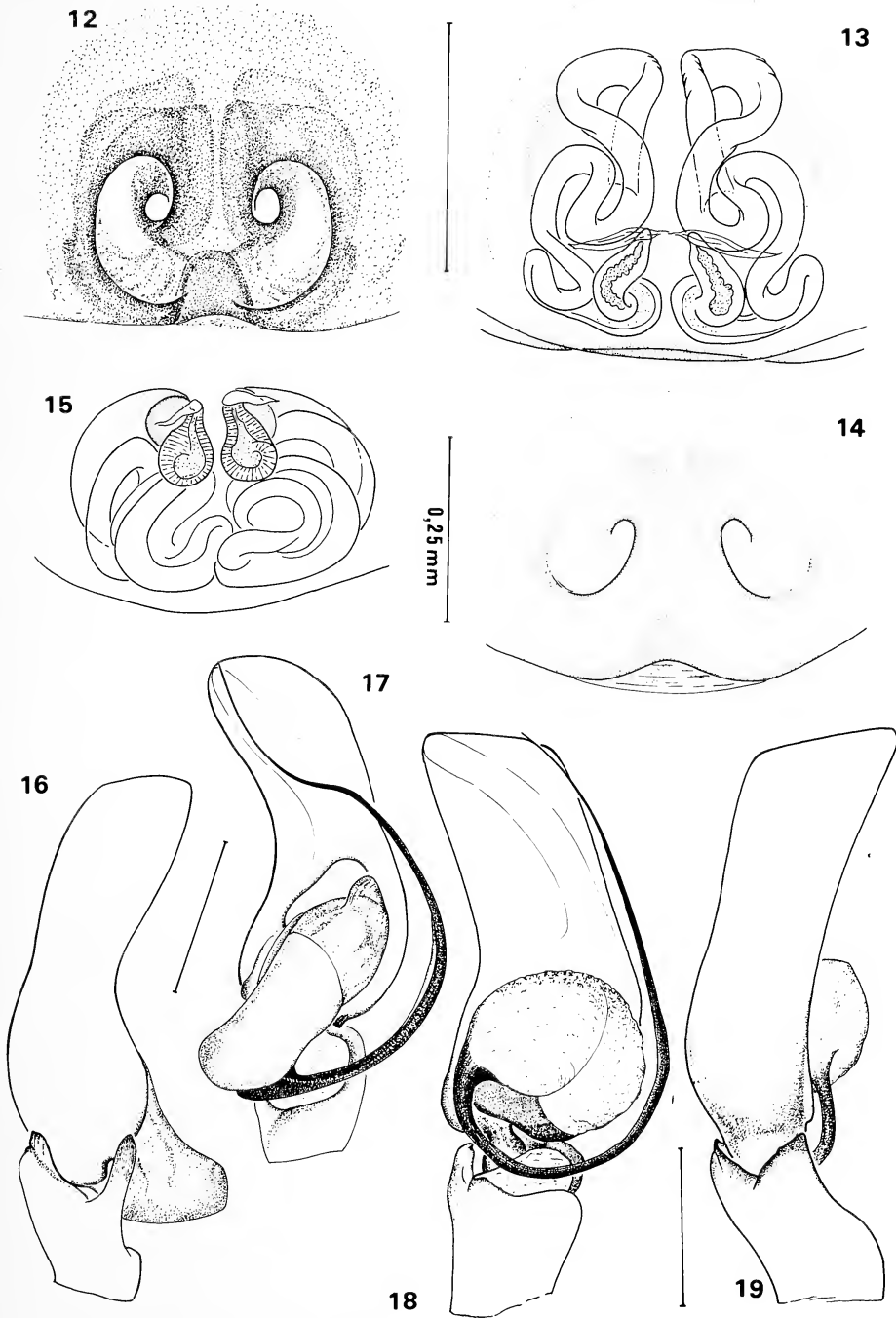
Cybele vincenti Peckham y Peckham 1893:696, t. 61 figs 4, 4a-d (macho y hembra sp.n.).

Eustiromastix vincenti: Simon 1903:724. (*Vincenti*); Petrunkevitch 1911:650; Roewer 1954:1079; Bonnet 1956:1843 (*vincentii*).

Redescripción del Holotipus macho.—Largo total 5,866. Prosoma: largo 2,766; ancho 2,333; alto 1,633. Clípeo: alto 0,100. Área ocular: largo 1,466. Ancho de la hilera anterior 2,166; de la posterior 2,133. Ojos de la 2a. hilera, equidistantes de O.L.A. y O.L.P. Diámetro de O.M.A. 0,700. Quelíceros: largos, con los dos tercios apicales divergentes. Surco unquéal largo y oblicuo; un diente pequeño en el ángulo del promargen; un diente reducido en la parte media del retromargen. Uña larga y algo flexuosa en la base. Patas: longitud relativa y espinas como en el género. Patella I sin espinas y tibia I con p l-l. Palpos: tarso largo y delgado, recto. Bulbo alargado, con ápice protuberante. Estilo largo, originado en la base, ubicado prolateralmente (Figs. 7 y 8). Opistosoma: largo 2,866.

Aspecto y color en alcohol.—Prosoma con los costados de la región cefálica algo convexos. Declive torácico pronunciado, inclinado a partir de O.L.P. Color pardo; región cefálica anaranjada. Declive torácico con una banda amarilla con pelos blancos. Lados del prosoma, con bandas submarginales de pelos blancos, desde la altura de O.L.P. hasta el espacio entre coxas II y III. Clípeo con fila de largos pelos blancos marginales, sin barba. Opistosoma pardo grisáceo con manchitas amarillas, con una banda media longitudinal amarilla, que en la mitad apical incluye 3 ó 4 bandas pardas transversas, con forma de acento circunflejo. Vientre pardo claro con manchas pardo oscuro. Patas I y II amarillas, con ápice de fémures, tibias y metatarsos, pardos. Palpos pardos, con ápice del tarso amarillo.

Descripción de la Hembra.—Prosoma: largo 2,133; ancho 1,700; alto 1,200. Clípeo: alto 0,100. Área ocular: largo 1,082. Ancho de la hilera anterior 1,616; de la posterior



Figs. 12, 13.—*Eustiromastix major*, hembra: 12, epigino; 13, espermatecas y conductos.

Figs. 14, 15.—*E. vincenti*, hembra: 14, epigino; 15, espermatecas y conductos.

Figs. 16, 17.—*E. moraballi*, macho: 16, palpo, retrolateral; 17, palpo, ventral.

Figs. 18, 19.—*E. intermedius* sp.n., Holotipus macho: 18, palpo, ventral; 19, palpo, retrolateral (Escala 0,5 mm, salvo indicación).

ojos de la 2a. hilera. En cada costado, en el espacio entre el ojo de la 2a. hilera y el O.L.P., una pequeña mancha de pelos blancos. Todas las manchas de pelos arriba mencionadas tienen color pardo anaranjado como fondo. Dos bandas marginales amarillas cubiertas de pelos blancos, que van desde la parte media de la coxa IV hasta debajo de O.L.A. y forman una barba ancha y densa en el clípeo. Quelíceros rojizos con pelos pardos. Hembra con igual diseño en dorso de opistosoma; vientre con ancha banda parda. Pata I pardo oscuro algo rojizo, patella y tibia con anillo pardo claro sub-basal con pelos blancos. En el resto de tibia y en metatarso, abundantes pelos pardos, largos y delgados, más abundantes en cara inferior. Patas III y IV con fémur amarillo, con anillo basal y apical, pardos; los otros artejos pardo claro, con parte media amarilla; tarso amarillo. Palpo con fémur y patella amarillos con largos pelos blancos dorsales; tibia y tarso pardo claro con pelos pardos, más largos en la cara prolateral. Tibias III y IV, con una espina dorsal basal.

Observaciones.—Los holotipos de *E. major* y *E. styliferus*, se redescubrieron en una publicación anterior (Galiano 1963). Las medidas de ambos ejemplares y la comparación de los palpos, muestran que la única diferencia reside en el mayor tamaño de *E. major*, y en la mayor longitud relativa del tarso del palpo con respecto al bulbo. Las descripciones originales de las dos especies distinguen a *styliferus* por la presencia de una mancha de pelos blancos en el borde anterior de la región cefálica. El estudio de un lote relativamente grande de ejemplares procedentes de Bahía, Brasil, ha permitido comprobar que existe gran variación en el tamaño del cuerpo; los machos miden de 6 a 9, 8 mm y las hembras de 7 a 9, 7 mm. Los machos de gran tamaño tienen los tarsos relativamente más alargados que los pequeños. En cuanto a las manchas de pelos, es común que desaparezcan en los ejemplares mal preservados, donde todos los pelos se han caído. Por estas razones, las dos especies se consideran sinónimos. No ha podido localizarse el tipo de *Theratoscirtus affinis* Caporiacco, pero la descripción y los dibujos que la acompañan, pese a sus deficiencias, demuestran que se trata de *E. major*. El ejemplar Holotypus macho de *E. styliferus* está acompañando por varias hembras cuya apariencia general y colorido son similares a los del macho, pero que pertenecen a dos especies diferentes, separables por la estructura del aparato genital. Una de ellas es posiblemente *Freya* sp. y la otra es *E. major*. Se describe por primera vez la hembra de la especie.

Localidad típica.—Brasil: Rio Salobro.

Material estudiado.—Un macho Holotypus de *E. major*; un macho Holotypus de *E. styliferus* y ejemplares no descriptos del mismo lote procedentes de Brasil, Amazonas (M.N.H.N.). Brasil, estado de Bahia: Lomanto Jr., Itamarajú, Ilheus, Ipanema, Coaraci, Jucari, 25 machos y 10 hembras (M.N.R.J.).

Eustiromastix keyserlingi (Taczanowski, 1879), nueva combinación
(Fig. 25)

Euophrys keyserlingi Taczanowski 1879:285 (hembra sp.n., *Keyserlingi*); Petrunkevitch 1911:647 (*keyserlingi*); Roewer 1954:1180; Bonnet 1956:1881.

Descripción del Lectotypus hembra.—Largo total 6,670 Prosoma: largo 3,300; ancho 2,566; alto 1,700. Clípeo: 0,166. Área ocular: largo 1,433. Ancho de la hilera anterior 2,233; de la posterior 2,200. Ojos de la 2a. hilera, separados de O.L.A. por 0,333 y de O.L.P. por 0,366. Diámetro de O.M.A. 0,700. Estría torácica: extremo anterior algo más adelante del borde posterior de O.L.P. Quelíceros: como en el género. Patas: longitud

1,532. Ojos de la 2a. hilera, separados de O.L.A. por 0,250 y de O.L.P. por 0,183. Diámetro de O.M.A. 0,516. Quelíceros: como en el género. Patas: longitud relativa y patas como en el género. Patella I sin espinas. Opistosoma: largo 2,733. Epigino: Figs. 14 y 15.

Aspecto y color en alcohol.—Esencialmente como el macho, pero con la banda media del prosoma más evidente.

Observaciones.—Debe hacerse notar que el material estudiado no tiene indicación de que se trate de los tipos. La etiqueta está escrita con lápiz y la localidad es ilegible. Sin embargo las estructuras de estos ejemplares corresponden a las descriptas por el autor, por lo que se considera que se trata del lote típico.

Localidad típica.—West Indies: St. Vincent.

Material estudiado.—Lote formado por 1 macho, 2 hembras y 2 juveniles (B.M.N.H.).

Eustiromastix moraballi Mello-Leitão, 1940
(Figs. 16, 17)

Eustiromastix moraballi Mello-Leitão 1940:185, figs. 19-20 (macho sp.n.); Roewer 1954:1079.

Descripción del Macho Nº 7118 M.A.C.N.—*Largo total:* 7,050. *Prosoma:* largo 3,333; ancho 2,800; alto 1,666. Clípeo: alto 0,200. Area ocular: largo 1,583. Ancho de las hileras anterior y posterior: 2,333. Ojos de la 2a. hilera, equidistantes de O.L.A. y O.L.P. Diámetro de O.M.A. 0,733. Quelíceros: prominentes en la parte basal de la cara anterior. Surco ungueal largo y excavado; retromargen con un diente; promargen con un diente grande en el ángulo. Patas: longitud relativa y espinas como en el género; Patella I con p 1 y tibia I con p 1-1. Palpos: bulbo alargado, protuberante en la base; estilo originándose en la parte basal prolateral (Figs. 16 y 17). Opistosoma: largo 3,666.

Aspecto y color en alcohol.—Prosoma pardo rojizo oscuro; región cefálica más clara. Declive torácico con una banda media amarillenta con algunos pelos blancos. Costados del prosoma negruzcos, sin rastros de bandas blancas. Pelos rojizos bajo los ojos laterales y un mechoncito de pelos blancos por fuera de cada O.M.A. Clípeo con algunos pelitos blancos, sin barba. Quelíceros rojizo oscuro, con abundantes pelos blancos en la base de la cara anterior. Opistosoma con una banda longitudinal media amarilla; vientre amarillo con manchitas pardas; tal vez haya existido una banda media más oscura. Pata I pardo rojizo negruzco, con la base de metatarso y el tarso, amarillentos. Patas II, III y IV, amarillas. Palpos amarillos, algo más oscuros en dorso de fémur y patella.

Observación.—Tibia I del Holotypus con v 1r-2-2.

Localidad típica.—British Guiana, Moraballi Creek, Essequibo River.

Distribución.—British Guiana. Venezuela.

Material estudiado.—Un macho Holotypus Nº 2494 (B.M.N.H.). Un macho Nº 7118 de Venezuela, Estado Miranda, Curupao (450 m) col. Bordon (M.A.C.N.).

Eustiromastix macropalpus, nueva especie
(Figs. 9-II, 23)

Diagnosis.—Especie próxima a *E. obscurus*; difiere por el palpo relativamente más grande con relación al cuerpo. El estilo, larguísimo, describe no menos de cuatro vueltas alrededor del bulbo. Patas III más largas que IV en ambos sexos.

Descripción del Holotypus macho.—Prosoma: largo 3,333; ancho 2,600; alto 1,933. Clípeo: alto 0,233. Área ocular: largo 1,566. Ancho de la hilera anterior 2,366; de la posterior 2,233. Ojos de la 2a. hilera separados de O.L.A. por 0,366 y de O.L.P. por 0,233. Diámetro de O.M.A. 0,800. Patas: longitud relativa III-IV-I-II. Espinas, como en el género. Patella I con p I y tibia I con p I-I-I. Tibias III y IV con d I basal. Palpos: tarso muy largo y ancho, doblado en ángulo recto hacia la cara ventral; dorsalmente aplanado, con una depresión retrolateral profunda y alargada. Bulbo disciforme, con estilo larguísimo, arrollado en cuatro vueltas a su alrededor habiendo además otras vueltas irregularmente dispuestas. Con palpos en posición normal, la punta doblada del tarso se sitúa por debajo del ápice de los quelíceros y los dos tarsos juntos cubren casi por completo el frente (Figs. 9, 10).

Aspecto y color en alcohol.—El Holotypus y los Paratypi están muy arruinados por la mala preservación. Los opistosomas se han arrugado y gran cantidad de pelo se ha caído, pero ciertas estructuras se conservan en buen estado. Ojos grandes, salientes. Color del prosoma pardo anaranjado; región cefálica cubierta por pelitos anaranjados. Región torácica con una banda media amarilla desde el extremo anterior de la estría torácica hasta la mitad del declive. Costados del prosoma con bandas angostas de pelos blancos con forma de U invertida, cuyos dos extremos se apoyan en el margen: uno a la altura de la coxa I y el otro a la altura de la coxa IV. Declive torácico con pelos pardo-negruzcos; un mechoncito de pelos blancos por fuera de cada O.L.A. y algunos pelitos blancos debajo de estos ojos. Clípeo glabro. Opistosoma muy arrugado; subsiste un mechón de pelos pardos basales (similares a los de *E. obscurus*). También parece distinguirse una banda media amarillenta. Patas amarillas, con manchas y anillos negruzcos. Pata I con pelos pardos largos y delgados en caras inferiores de fémur, patella, tibia y metatarso, que no forman fimbrias. Palpo pardo anaranjado.

Descripción del Paratypus hembra.—Largo total: 7,182. Prosoma: largo 2,933; ancho 2,333; alto 1,666. Clípeo: alto 0,166. Área ocular: largo 1,466. Ancho de la hilera anterior 2,200; de la posterior 2,066. Ojos de la 2a. hilera, separados de O.L.A. por 0,300 y de O.L.P. por 0,200. Diámetro de O.M.A. 0,733. Patas: longitud relativa III-IV-I-II. Espinas, como en el género. Tibias III y IV con d I basal. Opistosoma: largo aproximado 3,333. Epigino: Figs. 11, 23.

Aspecto y color en alcohol.—Esencialmente como el macho.

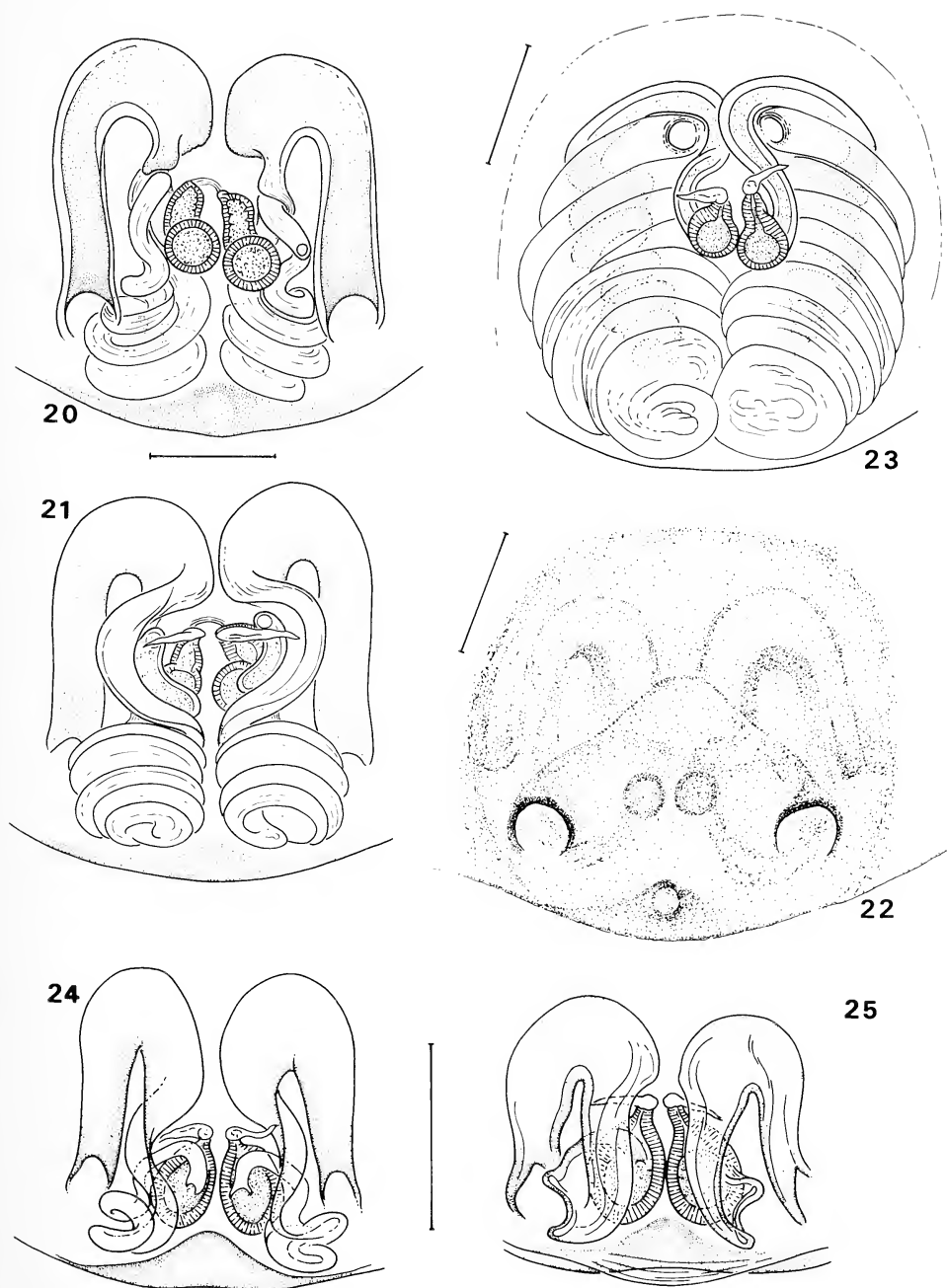
Localidad típica.—Brasil, Estado Ceará: Maranguape Mts.

Material estudiado.—Un macho Holotypus y una hembra Paratypus, col. Stanford Exp., W. Mann (M.C.Z.). Dos machos Paratypi Nº 7119 del mismo lote (M.A.C.N.).

Eustiromastix bahiensis, nueva especie
(Figs. 4-6, 20-22)

Diagnosis.—Especie próxima a *E. moraballi* y a *E. vincenti*; difiere por el bulbo ubicado en posición transversa con respecto al eje del tarso; tarso doblado en su mitad formando un ángulo de 90°; estilo más largo y espiralado en la parte distal que en las especies mencionadas.

Según el dibujo que se supone ilustra el palpo de *E. chaperi* (Simon 1903, fig. 861 I), *E. bahiensis* sp.n. sería también próxima a esta especie, diferenciándose porque en *E. chaperi* el clípeo posee una densa barba blanca, ausente en *E. bahiensis* sp.n. y porque en *E.*



Figs. 20-22.—*Eustiromastix bahiensis* sp.n., Paratypus hembra: 20, espermatecas y conductos, vista ventral; 21, los mismos, vista dorsal; 22, epigino.

Fig. 23.—*E. macropalpus* sp.n., Paratypus hembra: espermatecas y conductos, vista dorsal.

Fig. 24.—*E. obscurus?* hembra: espermatecas y conductos.

Fig. 25.—*E. keyserlingi* comb.n., Lectotypus hembra: espermatecas y conductos (Escala 0,25 mm).

chaperi los quelíceros son glabros, mientras que en *E. bahiensis* sp.n. los machos tienen un tubérculo en la cara anterior, cubierto por gruesos y erectos pelos pardo- negros.

Descripción del Holotypus macho.—Largo total 6,916. Prosoma: largo 3,200; ancho 2,666; alto 1,866. Clípeo: alto 0,200. Area ocular: largo 1,666. Ancho de la hilera anterior 2,333; de la posterior 2,266. Ojos de la 2a. hilera, equidistantes de O.L.A. y O.L.P. Diámetro de O.M.A.: 0,766. Quelíceros: paralelos, verticales. Cara anterior con una tuberosidad basal sobre la cual se insertan pelos pardo-negros, gruesos, erectos. Parte apical estriada transversalmente, con gruesos pelos pardos (Fig. 4). Patas: longitud relativa y espinas como en el género. Patella I con p I y tibia I con p I-I. Tibias III y IV con d I basal. palpos: fémur aplanado lateralmente en la base y dilatado hacia la cara inferior, con una pequeña depresión prolateral basal cuyos bordes tienen gruesos pelos pardos, curvos, regularmente dispuestos. Tarso doblado de modo que la mitad distal forma un ángulo de 90° con la proximal. Bulbo alargado, implantado perpendicularmente al eje longitudinal del tarso. Extremo prolateral membranoso y agudo; extremo.retrolateral da origen al estilo, muy largo y filiforme, curvado primero y luego espiralado. En posición normal, el estilo de cada palpo sobresale por delante del cuerpo del animal, formando dos amplios arcos muy visibles, que claramente distinguen a esta especie de las demás. (Figs. 5, 6). Opistosoma: largo 3,866.

Aspecto y color en alcohol.—Prosoma pardo rojizo oscuro; región cefálica negruzca, cubierta por pelitos sedosos, acostados, pardo-rojizos. Pelos rojizos bordeando los O.L.A. excepto un mechoncito de pelos blancos en el borde externo de cada uno de ellos. Margen anterior de la región cefálica con una banda transversa, angosta, de pelos blancos que se extiende entre la parte media de ambos O.M.A. Región torácica pardo negruzco, con pelos de igual color. No hay bandas marginales de pelos blancos; clípeo glabro, salvo unos pocos pelos pardos. Parte dorsal del prosoma con una gran mancha romboidal de pelos blancos cuyo vértice anterior llega a la altura del borde anterior de los O.L.P. y por detrás el extremo truncado termina en la mitad del declive torácico; vértices laterales en el límite entre las regiones cefálica y torácica. Quelíceros negruzcos. Opistosoma pardo con manchitas amarillas, con una ancha banda dorsal amarilla, cubierta de pelos blanco-amarillentos, que en la mitad apical incluye dos bandas pardas transversas, con forma de acento circunflejo; mitad basal con algunos pares de lunarcitos pardos. Bordeando la base del opistosoma y siguiendo por los lados, una banda amarilla con pelos blancos, que se pierde a la altura de la parte media. Costados con manchas pardas y abundantes manchas amarillas. Vientre amarillo con lunares pardos, más concentrados en la línea media, donde forman una difusa banda central. Patas I y II con fémur amarillo, más oscuro hacia el ápice; patella pardo claro, con bandas basal y apical, pardas; tibia pardo rojizo, negruzca apicalmente; metatarso pardo oscuro, con la parte media amarilla; tarso amarillo en la base, pardo en la mitad distal. Pata I con largos pelos pardos, delgados, en patella, tibia y metatarso, más abundantes en cara ventral, que no forman fimbrias. Zona amarilla de tibia con pelos blancos. Patas III y IV con fémures amarillos, algo pardos en el ápice; patellas, tibias y metatarsos amarillos, con anillos basales y apicales negruzcos; partes medias de los artejos con pelos blancos; resto con pelos pardos. Palpo amarillo con base rojiza; otros artejos pardo amarillento. Cara prolateral de tibia y tarso con largos pelos pardos; ápice de tarso con pelos blanco amarillentos.

Descripción del Paratypus hembra.—Largo total 7,847. Prosoma: largo 3,400; ancho 2,566; alto 1,666. Clípeo: alto 0,166. Area ocular: largo 1,550. Ancho de la hilera anterior 2,283; de la posterior 2,233. Ojos de la 2a. hilera, separados de O.L.A. por 0,400 y de O.L.P. por 0,333. Diámetro de O.M.A. 0,766. Quelíceros: base de cara anterior promi-

nente no forma tuberosidad como en el macho. Patas: longitud relativa y espinas como en el género. Patella I con p I y tibia I con p I-I. Opistosoma: largo 4,332. Epigino: Figs. 20, 22.

Aspecto y color en alcohol.—Esencialmente como el macho; difiere por lo siguiente: una ancha banda amarilla con pelos blancos desde el margen posterior hasta la altura de los ojos de la 2a. hilera; sus lados son paralelos hasta la altura de la estría, de allí se prolonga en la región cefálica como una punta de flecha. De cada lado envía una punta aguda en dirección a cada uno de los O.L.P. Esta banda es más larga y con puntas más agudas en hembras que en machos. Mechoncitos de pelos blancos en margen anterior, entre los O.M.A.; entre cada O.M.A. y O.L.A. respectivo; por fuera de cada O.L.A. y en el espacio entre cada O.L.P. y el ojo de la 2a. hilera. Algunos ejemplares con una manchita circular en medio de la región cefálica, en contacto con la punta de la banda media. No hay bandas laterales de pelos blancos, sino algunas manchas amarillas con pelos blancos. Una mancha bajo O.L.A. y otra a la altura de la coxa I. En algunos ejemplares hay otra mancha a la altura de la coxa II. Clípeo con fleco de largos pelos blancos marginales; el espacio bajo los O.M.A. desnudo. Resto del prosoma con pelos pardos, algo rojizos sobre región cefálica. Quelíceros pardos, con largos pelos blancos en cara anterior. Opistosoma como el macho. Patas I y II amarillas, con ápices de fémur y patella, pardos; tibia y metatarso con anillos apicales y basales, pardos. Patas III y IV con fémur amarillo, grisáceo en el ápice; patella amarilla con ápice pardo; tibia y metatarso pardos con parte media amarilla. Palpo con fémur amarillo; patella pardo claro; tibia y tarso pardos, con una mancha dorsal pardo oscuro y abundantes pelos pardo claro.

Localidad típica.—Brasil, Estado de Bahia: Lomanto Jr.

Material estudiado.—Un macho Holotypus y una hembra Paratypus de Brasil, Bahia, Lomanto Jr., col. Rory Goncalves; 5 machos y 7 hembras Paratypi, de Brasil, Bahia: Itabuna, Ilheus, Gandu (M.N.R.J.). Cinco machos y ocho hembras Paratypi, de Brasil, Bahia: Coaraci, Lomanto Jr. y Guaratinga (C.E.P.E.C.). Tres machos y cuatro hembras Paratypi Nº 7115 de Brasil, Bahia: Camacan y Jucau. Cinco machos Paratypi Nº 7120, de Brasil, Espírito Santo, Suoretama, col. A. Martínez X-1962 (M.A.C.N.). Tres machos y cuatro hembras Paratypi, de Brasil, Bahia, Lomanto Jr. y Jucau (M.E.G.).

Eustiromastix intermedius, nueva especie
(Figs. 18, 19)

Diagnosis.—Especie con caracteres intermedios entre *E. obscurus* y *E. vincenti*. Bulbo disciforme como en *E. obscurus*, estilo prolateral y tarso recto, como en *E. vincenti*. Difiere de otras especies del género porque la pata I del macho es más corta que la IV.

Descripción del Holotypus macho.—Largo total 7,980. Prosoma: largo 3,800; ancho 3,133; alto 2,133. Clípeo: alto 0,133. Area ocular: largo 1,950. Ancho de las hileras anterior y posterior: 2,633. Ojos de la 2a. hilera, equidistantes de O.L.A. y O.L.P. Diámetro de O.M.A. 0,833. Quelíceros: mitad basal fuertemente ensanchada en sentido transversal, con angulo externo saliente; mitad apical delgada con surco ungueal largo y excavado. Angulo del retromargen con un diente; promargen con dos dientes. Patas: longitud relativa IV-I-III-II. Espinas, como en el género. Patella I sin espinas y tibia I con p I-I. Palpos: tarso recto. Bulbo disciforme; estilo en posición prolateral (Figs. 18, 19). Opistosoma: largo 3,724.

Aspecto y color en alcohol.—Prosoma elevado, lados de la región cefálica algo convexos. Color pardo anaranjado; región torácica parda con una banda media cubierta de pelos blancos desde la estría al margen posterior. Pelos oculares rojizos. Clípeo con pelos

blancos en el margen debajo de O.M.A., que no forman barba. Prosoma sin bandas blancas laterales. Opistosoma con dorso pardo con lunares amarillos y una banda media amarilla, angosta, que en la mitad apical incluye 4 ó 5 banditas pardas transversas con forma de acento circunflejo. Lados del opistosoma amarillos con manchitas pardas. Vientre con una banda media, parda. Pata I parda, con cara prolateral negruzca; pelos pardos, delgados y largos, más abundantes en cara inferior de patella, tibia y metatarso, que no forman fimbrias. Tarso con algunos pelos blancos basales. Patas III y IV pardo claro, con anillos pardo oscuro en ápices de fémures, patellas, tibias y metatarsos y bases de tibia y metatarso. Quelíceros pardo anaranjado. Palpo pardo claro, con la cara dorsal de patella y tibia, pardo oscuro.

Observación.—Esta especie se ubica en *Eustiromastix* con ciertas dudas, pues el prosoma es más convexo en los lados que en las formas típicas, el área ocular es paralela y la pata I es más corta que la IV, caracteres anómalos dentro del género, al cual sin embargo parece pertenecer por la estructura del palpo. *E. intermedius* sp.n. tiene cierta semejanza con algunas especies del grupo *Viciriae* (Simon 1903:741) especialmente *Chira*, del cual se diferencia por tener la pata IV mucho más larga que la III y por la forma del palpo.

Localidad típica.—Venezuela, Parque Nacional de Aragua: Rancho Grande.

Material estudiado.—Un macho Holotypus N^o 7116, noviembre de 1968, col. M.E. Galiano (M.A.C.N.). Un macho Paratypus, de igual localidad y colector (M.E.G.).

ESPECIES EXCLUIDAS Y DUDOSAS

Eustiromastix rufohirtus Simon, 1902

Eustiromastix rufohirtus Simon 1902:417 (macho sp.n., *rufohirta*), 1903:730, fig 843 E; Petrunk-evitch 1911:650; Roewer 1954:1079; Bonnet 1956:1843; Galiano 1963:349, t. 18 figs. 14, 15.

Observación.—El aspecto general y colorido es similar al de las especies de *Eustiromastix*, pero la estructura del palpo, muy próxima a la de *Freya regia* demuestra que esta especie debe ser transferida como *Freya rufohirta* n. comb.

Localidad típica.—Brasil: Pará.

Material estudiado.—Un macho Holotypus (M.N.H.N.).

Eustiromastix pantherinus Mello-Leitão, 1942

Eustiromastix obscurus Mello-Leitão 1942:419, figs. 45, 46 (hembra, n.sp.) [no *E. obscurus* (Peckham y Peckham, 1893)].

Eustiromastix pantherinus Mello-Leitão 1942:420, figs. 47, 48 (hembra n.sp.); Roewer 1954:1079. **NUEVA SINONIMIA.**

Eustiromastix parobscurus Roewer 1951:450 [nom. nov. pro *E. obscurus* Mello-Leitão 1942 *praeoc.* sub *Cybele* = *E. obscurus* (Peckham y Peckham, 1893) Simon, 1902], 1954:1079. **NUEVA SINONIMIA.**

Observaciones.—En 1942, Mello-Leitão describió dos nuevas especies de *Eustiromastix* y pese a que el nombre estaba preocupado por la especie típica del género, llamó a la primera de ellas *E. obscurus*. Para corregir la homonimia resultante, Roewer (1951:450) dio a la especie el nuevo nombre de *E. parobscurus*.

En la presente contribución se establece que *E. obscurus* Mello-Leitão, 1942, y *E. pantherinus* Mello-Leitão, 1942 son sinónimos y por lo tanto, se adopta para la especie el nombre de *E. pantherinus* Mello-Leitão, 1942, que es el sinónimo más antiguo utilizable, en reemplazo de *E. obscurus* Mello-Leitão, 1942 que debe ser permanentemente desechado por tratarse de un homónimo primario y del nombre *E. parobscurus* Roewer, 1951, que es un sinónimo más reciente (Código de Nomenclatura Zoológica, art. 60a).

E. pantherinus Mello-Leitão, 1942 deberá ser excluida del género *Eustiromastix*, pues pertenece a otro taxon actualmente en estudio, que incluye especies como *Saitis uncifer* Tullgren y *Evophrys ancilla* Koch.

Localidad típica.—R. Argentina, provincia de Santiago del Estero, Asusques.

Material estudiado.—Una hembra Holotypus de *E. obscurus* Mello-Leitão Nº 15.555; una hembra Holotypus de *E. pantherinus* Mello-Leitão Nº 15.560 (M.L.P.).

Eustiromastix chaperi Simon, 1902

Eustiromastix chaperi Simon 1902: 417 (macho sp.n. *Chaperi*), 1903: 730, fig. 861 I; Petrunkevitch 1911: 649 (*chaperi*); Mello-Leitão 1941: 297; Roewer 1954: 1079; Bonnet 1956: 1843.

Observación.—El tipo de esta especie, que debería hallarse en el Muséum National d'Histoire Naturelle de Paris, no ha podido ser ubicado. Parece evidente que Simon confundió de alguna manera sus especies ya que el dibujo que aparece en 1903 con el número 861 I y cuya leyenda indica que es *E. major* no corresponde a dicha especie sino que a juzgar por la descripción debe tratarse del palpo de *E. chaperi*. Por sus características, *E. chaperi* se aproxima al grupo de especies de bulbo alargado y protuberante, junto a *E. vincenti*, *E. moraballi* y *E. bahiensis* sp.n. La especie será adecuadamente reconocida cuando se colecten otros ejemplares en la localidad típica.

Localidad típica.—Colombia: Naricual.

Eustiromastix guianae Caporiacco, 1954

Eustiromastix guianae Caporiacco 1954:176, figs. 65, 65 a (macho sp.n.).

Observación.—El tipo de esta especie no ha podido ser hallado. El palpo, según el dibujo publicado, no parece corresponder al del género. La pata III es considerablemente más larga que la pata IV, diferencia debida a la mayor longitud del fémur y tibia III, mientras que las patillas de ambas patas son iguales. Estas proporciones alejan a la especie de las formas típicas de *Eustiromastix* por lo que es posible que no pertenezca al género. Se la considera *species inquirendae*.

Localidad típica.—Guayana Francesa: Charvein.

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PSEUDOSCORPIONS OF THE FAMILY CHELIFERIDAE FROM OREGON (PSEUDOSCORPIONIDA, CHELIFEROIDEA)

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Abstract

A new genus, *Aspurochelifer*, and its type, *Aspurochelifer littlefieldi*, new species, are described from California, Idaho, Nevada, Oregon and Washington; the first Oregon state records are reported for *Dactylochelifer silvestris* Hoff, *Hysterochelifer fuscipes* (Banks), *H. proprius* Hoff, and *Parachelifer persimilis* (Banks); and new Oregon records are provided for *P. scabriculus* (Simon), *Chelifer cancroides* (Linnaeus) and *Haplochelifer philipi* (Chamberlin).

INTRODUCTION

Even though cheliferid pseudoscorpions are easily seen and occur almost worldwide, many species and even many genera are poorly characterized and have been reported from only scattered localities within their probable ranges. Of the approximately 40 species from the United States, only about one-half have been described in modern terms (Hoff 1945, 1946b, 1946c, 1949, 1950, 1956, 1964; Chamberlin 1949, 1952; Nelson 1975). Surprisingly, only a total of eight Oregon records (Banks 1895; Hoff 1950; Chamberlin 1952) are reported for the three previously known Oregon species: *Parachelifer scabriculus* (Simon), *Chelifer cancroides* (Linnaeus) and *Haplochelifer philipi* (Chamberlin). Yet, many cheliferid specimens from Oregon have accumulated through the years in the Benedict, Chamberlin, Malcolm, Muchmore, and Schuster Collections. In our attempt to determine these specimens to species, more than 500 specimens, including type series and specimens from other states, have been examined. The present paper provides descriptions of a new cheliferid genus and a new species; the first Oregon records for *Dactylochelifer silvestris* Hoff, *Hysterochelifer fuscipes* (Banks), *H. proprius* Hoff and

Parachelifer persimilis (Banks); and additional Oregon records for the three species previously known from Oregon. The resulting comparative morphological studies of the western North American species of *Hysterochelifer* Chamberlin and *Parachelifer* Chamberlin are being published separately.

A number of works, in addition to those cited above, contain major contributions to the present, though incomplete, knowledge of cheliferids. Chamberlin (1931) provided numerous illustrations in his comparative morphological monograph of the order; Beier (1932), the early synonymy of the family and a descriptive key to approximately 125 species of the world; Beier (1963), a descriptive key to nearly 20 European species; and Hoff (1958), a list of 26 cheliferid species from the United States and Canada and a highly useful key to tribes and genera. Oregon species of the family may be identified by the following key:

- 1. Coxal sacs absent in male; cribriform plates of female paired and as large in diameter as the diameter of the anterior tracheal trunks*Haplochelifer philipi*
Coxal sacs present in male; female with median cribriform plate single, or paired with diameter much smaller than diameter of anterior tracheal trunks 2
- 2. Coxal sacs of male with a well-defined atrium; female with a single median cribriform plate *Dactylochelifer silvestris*
Coxal sacs of male without an atrium; female with paired median cribriform plates; tribe Cheliferini (*the following couplets are based on males only*) 3
- 3. Males with tarsal claws of leg IV bearing an accessory tooth 4
Males with tarsal claws of leg IV simple, not toothed 6
- 4. Cheliceral hand lacking seta *sb* *Chelifer cancroides*
Cheliceral hand with seta *sb* present (genus *Parachelifer*) 5
- 5. Chela (exclusive of pedicel) less than 1.65 mm in length; movable finger shorter than hand *P. scabriculus*
Chela (exclusive of pedicel) 1.7 mm or more in length; movable finger longer than hand *P. persimilis*
- 6. Male with a well-developed antero-lateral process (spur) on margin of coxa IV; well-developed spurs present on at least tergites I to III (genus *Hysterochelifer*) . . 7
Male without an antero-lateral process; spurs absent on tergites, although lateral margin of tergite may appear very heavily sclerotized and darkly pigmented
. *Aspurochelifer littlefieldi*
- 7. Tarsus of leg I with 2-3 very enlarged setiferous tubercles at proximal end of a deep sinus; chela length (exclusive of pedicel) 1.10-1.50 mm; femur length 0.75-1.07 mm; chelal hand in lateral view slender, length/breadth ratio 4.0-4.7 . . *H. proprius*
Tarsus of leg I without enlarged setiferous tubercles, sinus shallow; chela length (exclusive of pedicel) 0.95-1.15 mm; femur length 0.65-0.76 mm; chelal hand in lateral view stout, length/breadth ratio 2.6-3.4 *H. fuscipes*

Tribe Cheliferini Chamberlin

The tribe Cheliferini (subfamily Cheliferinae Simon) has been well characterized by Hoff (1946a, 1956, 1958, 1964) and is represented in Oregon by five genera, including the one described below.

Aspurochelifer, new genus

Etymology.—The generic name refers to the absence of spurs on the tergites, carapace and coxae IV.

Diagnosis.—Of typical cheliferine facies; eyes present; cheliceral hand with 5 setae; tarsus of leg IV with simple, undivided claws and with dentate subterminal setae; claws of leg I of male asymmetrical with posterior claw dentate; movable finger of chela with 4 setae; fixed finger with normal number of setae, IT closer to ET than to EST; carapacial and tergal spurs absent; median cribriform plates of female paired, with diameter smaller than diameter of anterior tracheal trunks; males with coxal sacs and prominent apical spur on tarsi I, antero-lateral process (spur or minute tooth) on coxae IV absent.

Type species.—*Aspurochelifer littlefieldi*, new species.

Remarks.—Specimens of *Aspurochelifer* will key to *Hysterochelifer* in Beier (1932, 1963), but not in Chamberlin (1932) or Hoff (1946a, 1958). Although the new genus is closely related to *Hysterochelifer* as well as to *Phorochelifer* Hoff (1956), it differs from both in the arrangement of the chelal chaetotaxy and in the degree of expression of male sexual dimorphism. Seta IT of the fixed finger of the chela is midway between ET and EST in *Hysterochelifer*, somewhat closer to ET than to EST in *Aspurochelifer* and somewhat closer to EST than to ET in *Phorochelifer*. Males of *Aspurochelifer* lack lateral spurs on the tergites and carapace, while males of *Hysterochelifer* and *Phorochelifer* bear such spurs. Males of *Aspurochelifer* lack any type of antero-lateral process on coxa IV, while males of *Hysterochelifer*, on the other hand, bear a prominent, well-developed lateral spur, and those of *Phorochelifer* exhibit a minute tooth-like process in the same position as the coxal spur (Hoff 1956:20).

Unless one has examined cheliferid males with well-developed lateral spurs on the tergites and on the posterior disc of the carapace (e. g., specimens of the genera *Chelifer*, *Hysterochelifer*, *Parachelifer* or *Phorochelifer*), it may be difficult to decide if spurs are present or absent. A lateral spur (Chamberlin 1923), also referred to as "spine" (Banks 1909), "crest" (Chamberlin 1932, 1934, 1952) or "keel" (Hoff 1946a, 1956, 1964), is a posteriorly and dorsally protruding process located just dorsal to the edge of the lateral margin of the tergite or carapace. These spurs bear one to three small setae. Although this process is absent in *Aspurochelifer*, one or two setae are borne on the heavily sclerotized lateral margin of the tergite in a comparable position to the spur.

At present, only the type species from the western United States is assignable to this new genus, although the Chamberlin Collection contains two males from North Carolina which represent a second slightly larger undescribed species.

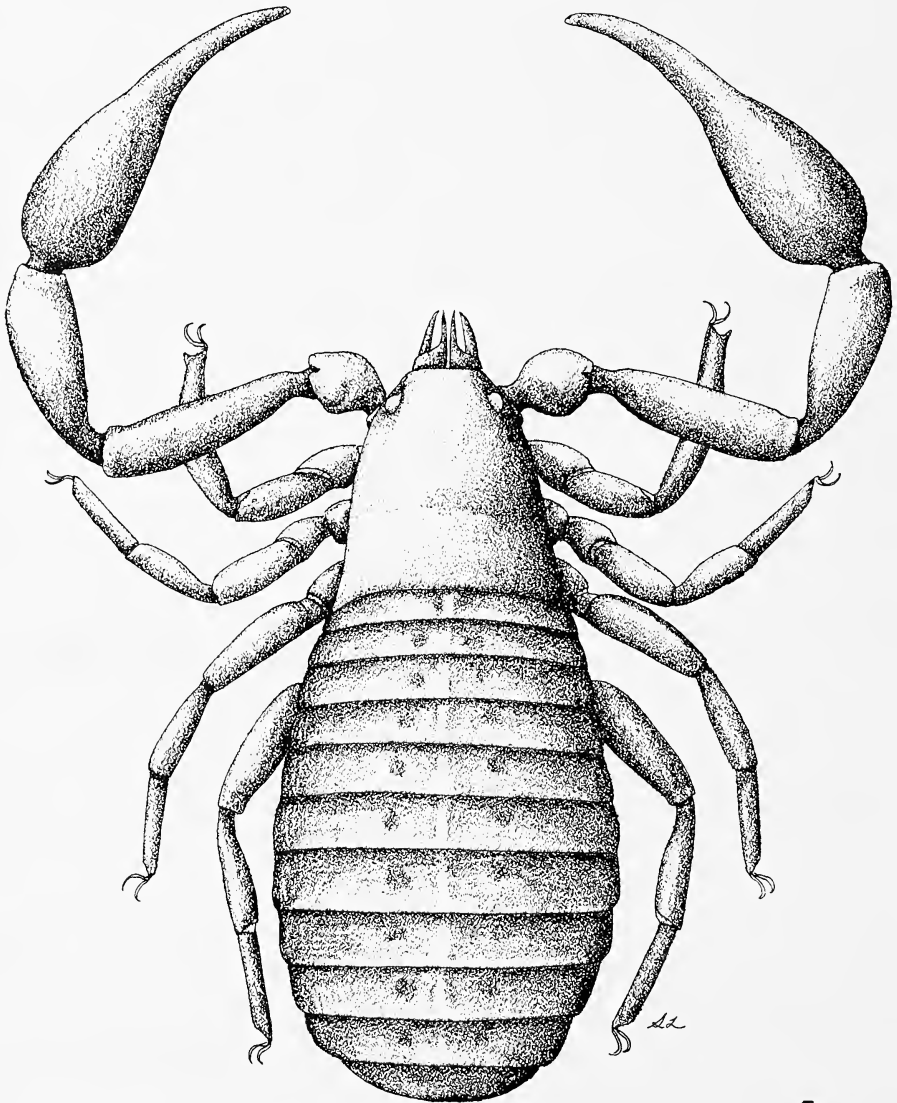
Aspurochelifer littlefieldi, new species

Figures 1-4

Type records.—Oregon; Jackson Co., Pinehurst, 9 September 1935 (R. V. Chamberlin and W. Ivie), 3 males (holotype AMNH, 2 paratypes JCC), 10 mi. E, 6 mi N of Gold Hill,

leaf litter of *Fraxinus latifolia* Benth., 14 September 1973 (E. M. Benedict), 2 males (paratypes EMB); Harney Co., 2 mi E of Frenchglen (1280 m), leaf litter of *Alnus tenuifolia* Nutt., 19 March 1972 (E. M. Benedict), 1 male (paratype EMB), 11 July 1972 (E. M. Benedict), 2 males, 3 females (paratypes EMB); Josephine Co., 1 mi S, 0.5 mi W of O'Brien, leaf litter of *Fraxinus latifolia*, 18 December 1971 (E. M. Benedict), 2 females (paratypes EMB).

Etymology.—The specific name is a patronym in honor of Carrol D. Littlefield of the Ecological Services of the United States Fish and Wildlife Service, Burns, Oregon.



1

Fig. 1.—*Aspurochelifer littlefieldi*, new species: 1, dorsal view of male.

Distribution.—Reported from California, Idaho, Nevada, Oregon and Washington.

Diagnosis.—Based on adults. Body length of male 2.07-2.75 mm, of female 2.46-2.82 mm; palpal femur length of male 0.68-0.78 mm, of female 0.71-0.78 mm; pedipalps relatively stout, fingers slightly longer than the relatively broad hand; male with an exceedingly shallow sinus on tarsus I.

Description.—Measurements in Table 1, morphometric ratios in Table 2. Derm generally coarsely granulate to grano-reticulate; setae clavate, except as noted.

Carapace (Fig. 1): subtriangular, slightly longer than greatest breadth; median and posterior furrows deeply impressed; median disc not impressed medially; posterior disc tergiform, medial area faintly impressed with derm slightly smoother but still as heavily sclerotized and pigmented as other areas; only a few moderately sized setiferous tubercles, especially laterally on ocular disc; holotypic chaetotaxy 4-8(60±); one pair of well-developed corneate eyes about one ocular diameter from anterior margin.

Coxal area: each coxa IV with a well-developed coxal sac; setal number inconstant between coxal pairs, holotypic chaetotaxy approximately 3-m-13:7:10:37:50.

Abdomen (Fig. 1): somewhat oblong; pleural membrane roughly striate; scuta of tergites I to X more or less divided by narrow, deeply impressed and heavily sclerotized granulate intratergal membranes; lateral margins of tergites I to III heavily sclerotized but lacking spurs; derm of anterior sternites somewhat smoothly reticulate, becoming more granular posteriorly; sternal scuta IV to X completely divided, XI partially divided; abdominal setae uniseriate except for 1 or 2 setae along lateral margin of tergite; setae mostly simple except bifurcate or monodentate around genital opening, holotypic chaetotaxy of tergites 11:12:11:10:14:11:12:12:13:11:9:2, of sternites 75±:[0-0]:(0)4-4/19(0):(1)9(1):11:10?:9:9:10:8:11:2; sexual structures of cheliferine facies, ramshorn organ normal, sclerotic rod of stumen convolutum not extending beyond anterior invagination. Female genitalia typical.

Chelicera: galea long, with a total of 6 terminal and subterminal rami; lamina exterior a broad marginal band; serrula exterior with 15 to 17 blades; serrula interior with 3 dentate lobes distal to basal velum; flagellum of 3 setae, anterior seta with 6 to 7 spinules (may appear simple in certain orientations); hand with 5 acuminate setae; apical tooth of fixed finger with 3 microdenticles along inner margin, succeeded by 3 to 5 retrorse marginal teeth; apical tooth of movable finger weakly bifid terminally, subapical lobe well-developed and conical.

Pedipalp (Figs. 1-2): robust; trochanter with a moderately developed, lateral-dorsal protuberance bearing a moderately large setiferous tubercle. Chelal chaetotaxy and dentition as illustrated in Figs. 2-3; fixed finger with 42-47 and movable finger with 40-50 marginal teeth.

Legs (Fig. 1): relatively stout; derm grano-reticulate to reticulate; tarsus I (Fig. 4) not markedly swollen along extensor margin proximal to shallow sinus; claws of leg I asymmetrical, anterior one of normal appearance, posterior one modified with a slender tooth (Fig. 4).

Remarks.—The bifurcate nature of the setae surrounding the male genital opening is often destroyed by KOH treatment (e.g., in the holotype). These delicate branches are not destroyed on specimens mounted in Hoyer's medium (e.g., EMB paratypes).

Habitat.—Known only from leaf litter of thinleaf alder and Oregon ash.

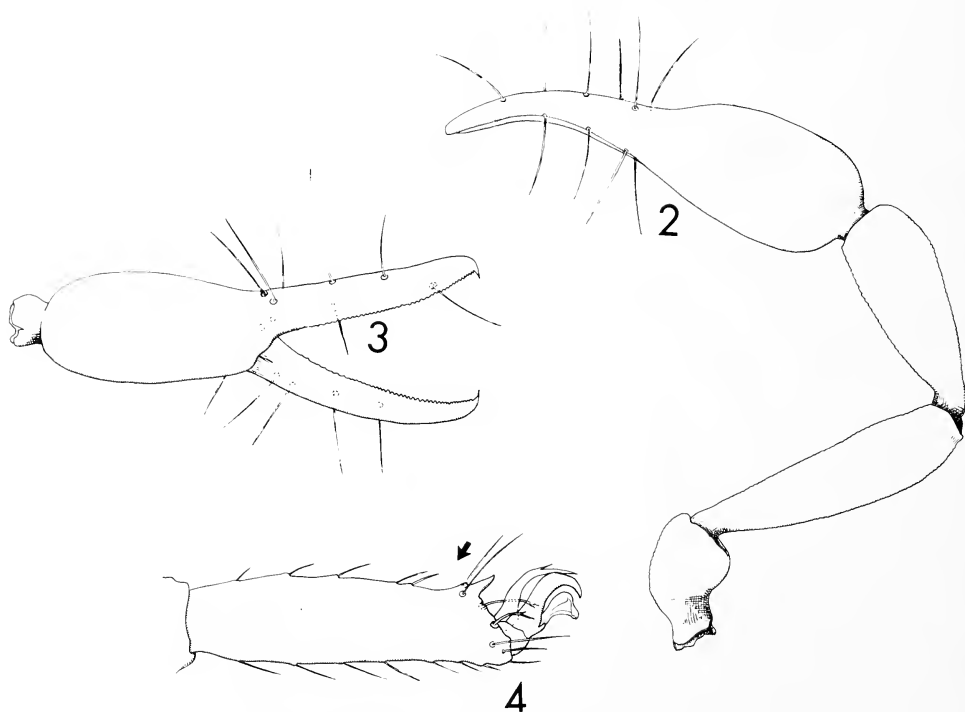
Other specimens examined.—*California*: Bray, 8 September 1935 (W. Ivie and R. V. Chamberlin), 1 male (JCC); *Marin Co.*, Bolinas, 24 March 1960 (R. O. Schuster), 1 male, 1 female, 3 nymphs (ROS), 7 April 1960 (R. O. Schuster), 3 nymphs (ROS); *Mendocino Co.*, Ukiah, 12 July 1937 (R. V. Chamberlin), 1 male (JCC); *Orange Co.*, 2 mi N of Laguna, 13 June 1960 (H. H. McKenzie), 1 male, 3

females, 3 nymphs (ROS); *Sierra Co.*, 3 mi S Sierraville, September 1961 (W. Ivie and W. J. Gertsch), 8 males, 5 females (ROS); *Siskiyou Co.*, Weed, 8 September 1933 (R. V. Chamberlin and W. Ivie), 1 male (JCC); *Solano Co.*, Suisun, October 1955 (K. H. Haller), 1 male (CCH); *Idaho*; *Idaho Co.*, Kooskia, Clearwater Creek, 23 August 1940 (W. Ivie), 1 male (JCC); *Nevada*; *Washoe Co.*, Verdi, 11 July 1937 (R. V. Chamberlin), 1 male (JCC); *Washington*; *Yakima Co.*, White Swan, 16 April 1933 (C. W. Getzendaner), 1 male (JCC), 21 May 1933 (J. Wilcox), 1 male (JCC).

Chelifer cancroides (Linnaeus)

Early references to this widely distributed and well-known species can be traced through the annotated synonymy of Beier (1932); more recent references are given by Nelson (1975). Chamberlin (1932) and Hoff (1956) have characterized this monotypic genus in modern terms. Keys by Hoff (1958, 1959) are especially useful for separating this species from other closely related forms which inhabit Oregon.

Even though *C. cancroides* was collected in Oregon, at least as early as 1921, surprisingly, the only published records to date are two, one each from Jackson and Tillamook Counties (Hoff 1950). Therefore, to document its wide distribution throughout the state, one record per county and/or records with habitat data are given below.



Figs. 2-4.—*Aspurochelifer littlefieldi*, new species: 2, dorsal aspect of pedipalp of paratype male; 3, internal aspect of chela of paratype male; 4, lateral aspect of tarsus I of holotype male (note very shallow sinus, at arrow).

Table 1.—Measurements (in mm) of *Aspurochelifer littlefieldi*, new species from California, Idaho, Nevada, Oregon and Washington (Abbreviations: B=breadth; D=depth; L=length).

	♂♂	♀♀
Body L	2.07-2.75	2.46-2.82
Abdominal B	0.96-1.08	1.13-1.18
Carapace L	0.69-0.76	0.80-0.86
Ocular B	0.37-0.41	0.43-0.44
Posterior B	0.73-0.82	0.83-0.84
Eye diameter	0.07-0.10	0.07-0.10
Chelicera L/B	0.20-0.28/0.12-0.16	0.23-0.26/0.13-0.14
Pedipalp		
Trochanter L/B	0.35-0.37/0.19-0.22	0.37-0.38/0.22-0.23
Femur L/B	0.68-0.78/0.17-0.19	0.71-0.78/0.20-0.21
Tibia L/B	0.63-0.17/0.20-0.22	0.66-0.74/0.24-0.25
Chela L/B	1.11-1.26/0.31-0.34	1.18-1.31/0.35-0.36
Chela D	0.28-0.32	0.34-0.35
Movable finger L/Hand L	0.51-0.64/0.56-0.68	0.60-0.70/0.59-0.62
Leg I		
Entire femur L/D	0.44-0.48/0.12-0.15	0.47-0.51/0.13-0.15
Tibia L/D	0.30-0.33/0.09-0.11	0.32-0.33/0.08-0.10
Tarsus L/D	0.30-0.33/0.08-0.09	0.34-0.35/0.06-0.07
Leg IV		
Entire femur L/D	0.57-0.63/0.17-0.19	0.65-0.70/0.19-0.21
Tibia L/D	0.42-0.48/0.10-0.11	0.48-0.51/0.11-0.13
Tarsus L/D	0.37-0.41/0.07-0.08	0.41-0.43/0.08-0.09

New records.—Oregon; *Baker Co.*, 10 mi W of Baker, 7 August 1963 (J. S. Buckett), 1 male (ROS); *Benton Co.*, Corvallis, on human in bathroom, 26 May 1935 (N. Larson and Wheeler), 1 male, 1 female (JCC), Corvallis, soapdish in bathroom, 20 March 1937 (D. Edwards), 1 female (JCC), Corvallis, college building, 14 June 1937 (V. Shattuck), 1 male (JCC), Corvallis, house, 20 April 1940 (E. Crumb), 2 females (JCC), 0.5 mi NW of Glenbrook, *Neotoma* sp. debris in old shed, 4 December 1971 (E. M. Benedict), 2 nymphs (EMB); *Clackamas Co.*, Wilsonville, house, May 1938 (G. Danforth), 1 male, 1 female (JCC); *Coos Co.*, Bayview, in old book, 5 November 1938 (J. Briggs), 1 female (JCC); *Harney Co.*, 32 mi SE of Burns, bathtub, July 1972 (C. Gniewosz), 1 female (EMB), 32 mi SE of Burns, hay-dung in barn, 9 July 1972 (E. M. Benedict), 2 nymphs (EMB), 1 mi E of Frenchglen, hay-dung in barn, 12 May 1972 (E. M. Benedict), 1 male, 8 nymphs (EMB), 1 mi E of Frenchglen, hay-dung in barn, 11 July 1972 (E. M. Benedict), 4 nymphs (EMB); *Jackson Co.*, Medford, 7 July 1935 (L. G. Gentner), 1 female (JCC); *Klamath Co.*, Merrill, 15 April 1962 (J. D. Vestres), 1 male (DRM); *Lane Co.*, 2.5 mi N of Cheshire, hay, mouse and barn swallow nests in old sheep shed, 4 December 1971 (E. M. Benedict), 5 males, 4 females, 5 nymphs (EMB); *Marion Co.*, Salem, dead peach limb, 15 September 1945 (J. Schuh), 1 male (JCC); *Multnomah Co.*, Gresham, bed, 10 June 1944 (J. Schuh), 1 female (JCC), Portland, Oregon Museum of Science and Industry, hay-dung from cow exhibit, May 1975 (G. Mills), 3 males, 1 nymph (EMB), Portland, bathtub, May 1976 (R. Pope), 1 male (EMB); *Wasco Co.*, The Dalles, house, 23 May 1939 (D. C. Mote), 1 female (JCC); *Washington Co.*, Forest Grove, October 1921 (no. coll.), 2 males, 2 females (JCC), Forest Grove, under old shingles of garage roof, September 1942 (J. C. Chamberlin), 1 male (JCC), 0.2 mi E of Sherwood, hay-dung in barn, 1 January 1972 (E. M. Benedict), 1 male, 1 female, 13 nymphs (EMB); *Yamhill Co.*, McMinnville, grass clippings, August 1941 (K. Fender), 1 male (JCC), 2 mi S of Carlton, hay-dung in barn, 1 January 1972 (E. M. Benedict), 1 specimen (EMB).

Haplochelifer philipi (Chamberlin)

Chamberlin erected the genus *Haplochelifer* in 1932 and designated *Chelifer philipi* Chamberlin, initially described in 1923 from California, as type species. He later (1952)

Table 2.—Morphometric ratios of *Aspurochelifer littlefieldi*, new species from California, Idaho, Nevada, Oregon and Washington (Abbreviations: B=breadth; D=depth; L=length).

	♂ ♂	♀ ♀
Pedipalp		
Femur L/B	3.7-4.2	3.5-3.8
Tibia L/B	2.9-3.2	2.7-2.9
Chela L/B	3.4-3.8	3.2-3.6
Chela L/D	3.9-4.2	3.5-3.7
Movable Finger L/Hand L	1.0-1.1	1.0-1.1
Hand L/B	1.7-2.0	1.6-1.7
Leg I		
Entire femur L/D	3.1-3.7	3.4-3.6
Tibia L/D	3.0-3.6	3.4-3.7
Tarsus L/D	3.4-4.1	4.8-5.1
Leg IV		
Entire L/D	3.1-3.5	3.5-3.6
Tibia L/D	4.1-4.5	4.0-4.2
Tarsus L/D	4.8-5.3	4.7-4.8

redescribed this monotypic genus and its type species in great detail; Hoff (1956) briefly characterized the genus and included it in his valuable key of 1958.

The species has been reported from a number of widely scattered localities in the western United States (Chamberlin 1923, 1952; Hoff 1956, 1961). Chamberlin (1952) gave the first records for Oregon from a total of five localities in Josephine, Jackson, Klamath and Malheur Counties. The new specimens from 25 localities in these and five additional counties are as variable in size as those described earlier by Chamberlin.

Specimens examined.—California; Santa Clara Co., Palo Alto, Stanford University, 29 March 1921 (J. C. Chamberlin), 1 male (holotype JCC), 1 female (allotype JCC); Oregon; Baker Co., 7 mi N, 8 mi E of Halfway (915 m), leaf litter of *Pinus ponderosa* Dougl. ex Loud., 17 September 1975 (E. M. Benedict), 1 male (EMB); Benton Co., Corvallis, under rock, 15 June 1898 (no coll.), 1 female (BMUW); Deschutes Co., 4.5 mi N, 3 mi W of Sisters (975 m), leaf litter of *P. ponderosa*, 22 March 1972 (E. M. Benedict), 1 male, 3 females, 2 nymphs (EMB), 11 mi SE of Bend (1070 m), leaf litter of *Juniperus occidentalis* Hook., 11 May 1972 (E. M. Benedict), 2 females, 1 nymph (EMB), 5 mi S, 1 mi E of Bend, leaf litter of *P. ponderosa*, 20 May 1972 (E. M. Benedict), 2 males, 2 females, 8 nymphs (EMB), leaf litter of *Arctostaphylos patula* Greene, 20 May 1972 (E. M. Benedict), 1 male, 1 female (EMB), 1 mi N of Bend, leaf litter of *P. ponderosa*, 1 October 1972 (E. M. Benedict), 2 males, 3 females, 1 nymph (EMB), leaf litter of *J. occidentalis*, 1 October 1972 (E. M. Benedict), 1 male, 1 female (EMB); Douglas Co., 3 mi SE of Tiller (425 m), leaf litter of *P. ponderosa*, 6 November 1971 (E. M. Benedict), 2 males (EMB), 15 mi NW of Glide (185 m), leaf litter of *Arbutus menziesii* Pursh, 1 April 1972 (E. M. Benedict), 1 male, 1 female, 5 nymphs (EMB); Harney Co., 11 mi SE of Riley (1340 m), leaf litter of *J. occidentalis*, 15 May 1972 (E. M. Benedict), 1 female (EMB), 13 mi S, 6 mi W of Princeton (1280 m), leaf litter of *J. occidentalis*, 14 July 1972 (E. M. Benedict), 1 male, 1 female, 1 nymph (EMB), 2 mi E of Frenchglen (1280 m), on top of rock under *J. occidentalis*, 15 May 1970 (C. D. Littlefield), 1 female (DRM), leaf litter of *J. occidentalis*, 11 July 1972 (E. M. Benedict), 1 male, 2 nymphs (EMB), leaf litter of *J. occidentalis*, 26 January 1974 (E. M. Benedict), 1 male, 1 female (EMB), leaf litter of *Prunus virginiana* L., 26 January 1974 (E. M. Benedict), 2 males, 6 females, 9 nymphs (EMB), Alvord Basin, Fifteen Cent Lake (1280 m), under rock about 10 m above shore, 27 April 1974 (L. Russell), 1 female

(EMB); *Jackson Co.*, 1 mi S of Ruch (520 m), leaf litter of *Quercus garryana* Dougl., 13 November 1971 (E. M. Benedict), 3 males, 2 females, 3 nymphs (EMB), 7 mi E, 3 mi N of Ashland (1070 m), under board, 23 March 1962 (J. Schuh and J. D. Vestres), 1 male (DRM), leaf litter of *Q. garryana*, 27 December 1971 (E. M. Benedict), 1 female (EMB), 2 mi N, 6 mi E of Ashland (975 m), leaf litter of *P. ponderosa*, 27 December 1971 (E. M. Benedict), 2 females (EMB), 10 mi E, 6 mi N of Gold Hill (395 m), leaf litter of *Q. garryana*, 22 January 1972 (E. M. Benedict), 3 females, 2 nymphs (EMB), 4 mi E of Eagle Point (425 m), leaf litter of *Q. kelloggii* Newberry, 22 January 1972 (E. M. Benedict), 1 female, 2 nymphs (EMB), 10 mi NW of Central Point (365 m), leaf litter of *Arctostaphylos* sp., 22 January 1972 (E. M. Benedict), 2 females, 1 nymph (EMB), 4 mi S, 11 mi E of Ashland (1465 m), leaf litter of *Quercus* sp., 15 October 1972 (E. M. Benedict), 2 females, 3 nymphs (EMB); *Josephine Co.*, 0.3 mi E of O'Brien (425 m), leaf litter of *Arctostaphylos* sp., 18 December 1971 (E. M. Benedict), 1 female, 3 nymphs (EMB), 0.5 mi E, 5.5 mi N of Galice (245 m), *Quercus chrysolepis* Liebm., 8 April 1972 (E. M. Benedict), 1 male, 1 nymph (EMB), 10 mi W of Selma (365 m), leaf litter of *Quercus garryana* 9 August 1973 (E. M. Benedict), 5 males, 1 female, 2 nymphs (EMB); *Klamath Co.*, Wocos, under board, 27 April 1971 (J. Schuh), 4 males, 1 female (DRM), Upper Klamath Lake, Algoma, ground litter, 17 April 1962 (J. Schuh), 2 males (DRM), Bly Mountain, 1 April 1962 (J. Schuh), 4 males (DRM).

Hysterochelifer fuscipes (Banks)

Our comprehensive study of the western North American species of *Hysterochelifer* Chamberlin reveals that Oregon specimens are assignable to two species, *H. fuscipes* and *H. proprius*, neither reported previously from Oregon. Chamberlin (1932) established the genus *Hysterochelifer* with *Chelifer fuscipes* Banks (1909) from California as type species. Even though there have been a number of references to this species (Banks 1909; Moles 1914; Chamberlin 1923, 1932; Beier 1932; Hoff 1958), it is very incompletely described, a deficiency which will be corrected in our revision of the western species of the genus, to be reported later.

Although both Moles and Chamberlin apparently examined new material from California, they did not list specimens. Therefore, it appears that the only prior published specimen record of this species is that of the type collection from Claremont, California (Banks 1909). Obviously, the three records below constitute the first records for Oregon.

Specimens examined.—*California*; *Los Angeles Co.*, Claremont, prior to 1909 (Baker), 2 males (syntypes MCZ); *Oregon*; *Benton Co.*, Corvallis, in sweeping, 7 May 1936 (N. Larson), 1 female (JCC), Corvallis, from freshly felled *Abies grandis* (Dougl.) Lindl. log, 21 July 1961 (R. G. Mitchell), 1 male, 1 female (DRM), 8 mi S of Corvallis, in moss on silver maple, 15 October 1940 (J. Schuh), 1 female (JCC).

Hysterochelifer proprius Hoff

Hoff (1950) described this species in great detail and later added supplemental details and new records (Hoff 1956, 1958, 1959, 1961). Prior to the present study, *H. proprius* had been considered uncommon (Hoff 1961) as it had been reported only from a total of 11 specimens collected in Arizona, New Mexico, and Colorado. The first records for Oregon are now reported from 22 localities.

Specimens examined.—*Arizona*; *Coconino Co.*, Flagstaff, 30 April 1936 (no. coll.), 1 male (holotype AMNH), 1 female (allotype AMNH); *Oregon*; *Benton Co.*, bark of *P. ponderosa*, 18 January 1939 (J. D. Vestres), 1 female (JCC); *Crook Co.*, near Prineville, *P. ponderosa* with *Dendroctonus brevicornis* Le Conte, no date (W. J. Buckhorn), 1 male (JCC); *Deschutes Co.*, 1 mi N of Bend, bark of *P. ponderosa*, 1 October 1972 (E. M. Benedict), 1 male, 1 nymph (EMB); *Grant Co.*, 3.9 mi E. of Dayville, bark of *Juniperus occidentalis*, 9 April 1937 (J. C. Chamberlin), 1 male, 1 female (JCC); *Harney Co.*, Cougar Creek, 17 October 1968 (J. Schuh), 1 female (DRM), 2 mi E of Frenchglen (1280 m), surface of rock under *J. occidentalis* tree, 15 May 1970 (C. D. Littlefield), 1 female (DRM), *J. occidentalis* bark, 18 March 1973 (E. M. Benedict), 1 male (EMB), 26 January 1974 (E. M. Benedict),

1 male (EMB), 11 mi E of Riley, bark of *J. occidentalis* tree, 15 May 1972 (E. M. Benedict), 8 nymphs (EMB), Diamond Craters, bark of *J. occidentalis* tree, 14 July 1972 (E. M. Benedict), 3 males, 5 nymphs (EMB), 16 mi N of Burns, bark of *P. ponderosa* tree, 17 July 1972 (E. M. Benedict), 1 male (EMB); Hood River Co., Hood River, no date (R. V. Chamberlin), 1 female (JCC); Jefferson Co., 4 mi E of Redmond, beating *Betula* sp., 28 May 1948 (J. Beer and V. Roth), 1 female (JCC); Klamath Co., near Klamath Falls, *J. occidentalis* bark, no date (J. C. Chamberlin), 3 males, 2 females (DRM), Klamath Falls, Geary Ranch, beating *Pinus* sp., 28 April 1955 (J. Schuh), 7 males, 1 female, 1 nymph (DRM), Klamath Falls, 12 September 1956 (J. Schuh), 1 male, 1 female (WBM), Malone Springs, 12 June 1962 (J. D. Vestres), 2 females (DRM), 7.4 mi E of Dairy, bark of *J. occidentalis*, 7 April 1937 (J. C. Chamberlin), 1 male, 1 female (JCC), Keno, bark of *J. occidentalis*, 7 April 1937 (J. C. Chamberlin), 2 males, 2 females, 4 nymphs (JCC); Lake Co., 5 mi N of Silver Lake, bark of *J. occidentalis*, 8 April 1937 (J. C. Chamberlin), 1 male, 1 female (JCC); Wasco Co., 1 mi S, 13 mi W of Simnasho, bark of *P. ponderosa*, 4 September 1938 (R. L. Prentiss, J. C. Chamberlin), 2 males, 1 female (JCC), 8 mi E, 3 mi N of Pine Grove, bark of *J. occidentalis* tree, 27 February 1974 (E. M. Benedict), 1 male (EMB).

Parachelifer scabriculus (Simon)

Chamberlin (1932) erected the genus *Parachelifer* and designated *Chelifer scabriculus* Simon (1878) from California as type species. In 1952, Chamberlin revised the generic diagnosis and clearly separated *Parachelifer* from the closely related genus *Chelifer*; Hoff (1956, 1964) also briefly characterized it. Of the approximately 15 species assigned to the genus (Hoff 1964), many are still inadequately defined by modern standards. This is true of most of the western North American species despite the comparative study of three species, including *P. scabriculus*, by Gering (1948).

Banks (1895) has reported the only record to date of *P. scabriculus* from Oregon based on a single specimen collected at Hood River (without habitat data). Chamberlin (1952) published a redescription of *P. scabriculus* based, not upon type specimens, but on a number of specimens collected at various sites in California. The three Oregon specimens, listed below, are clearly conspecific with a male and female from Santa Clara, California, from the Chamberlin series. Even though *P. scabriculus* was redescribed in detail, it is difficult to separate from other closely related species which lack modern descriptions. Thus, any identification of Oregon specimens should be regarded as tentative. As the species are now defined, Oregon specimens are separable by Hoff's (1958, 1959) keys into *P. scabriculus* and *P. persimilis*. Further study may reveal that the Oregon specimens actually belong to a single highly variable species instead of the two species to which they are currently assigned.

Specimens examined.—California; Santa Clara Co., Stanford University, 19 December 1921 (L. Kiler and E. Sette), 1 male, 1 female (JCC-168); Oregon; Jackson Co., 3 mi S, 11 mi E of Prospect (1160 m), bark of *Pinus lambertiana* Dougl., 22 August 1972 (E. M. Benedict), 1 male (EMB); Josephine Co., 0.5 mi E, 5.5 mi N of Galice, (152 m), bark from snag of *Pseudotsuga menziesii* (Mirb.) France, 8 April 1972 (E. M. Benedict), 1 male (EMB); Lane Co., 20 mi S, 14 mi E of Oakridge (1525 m), bark of *P. menziesii*, 16 August 1973 (E. M. Benedict), 1 female (EMB).

Parachelifer persimilis (Banks)

As implied above, this 1909 species of Banks lacks a modern description despite the many references to it in the literature (Banks 1909; Chamberlin 1923, 1932; Hoff 1950, 1956, 1959, 1961, 1963). The records below are the first for Oregon.

Specimens examined.—New Mexico; San Miguel Co., Pecos, prior to 1909 (N. Banks), 7 syntypes (MCZ); Oregon; Crater Lake National Park, Sleepy Hollow, phoretic on cerambycid beetles (*Ortholeptura valida* Le Conte), 8 August 1960 (D. H. Huntzinger), 1 male (DRM), 10 August 1960 (D. H. Huntzinger), 1 female (DRM), 17 August 1960 (D. H. Huntzinger), 1 female (DRM); Clatsop Co., 2 mi E of Elsie, phoretic on cerambycid, 31 August 1963 (coll. unknown), 1 male (DRM); Deschutes Co., Camp Abbott, 7 May 1944 (P. H. Arnaud), 7 males, 3 females (ROS), 1 mi N of Bend (1065 m), bark of *Pinus ponderosa*, 1 October 1972 (E. M. Benedict), 1 male, 1 nymph (EMB); Harney Co., 16 mi N of Burns (1550 m), bark of *P. ponderosa*, 17 July 1972 (E. M. Benedict), 1 male (EMB); Klamath Co., Klamath Falls, under bark, 2 May 1953 (J. Schuh), 2 males, 4 females (DRM), 8 May 1953 (J. Schuh), 1 male, 1 female (DRM), 21 February 1955 (J. Schuh), 6 males, 2 females (DRM), Upper Klamath Lake, under bark, 17 May 1955 (J. Schuh), 3 males, 2 females, 3 nymphs (DRM), 22 May 1955 (J. Schuh), 1 female (DRM); Lake Co., Hart Mt., Blue Sky, bark of *P. ponderosa*, 9 July 1976 (K. P. Shea), 1 male (EMB), phoretic on a cerambycid beetle (*Brachyleptura canadensis* Kirby), 26 July 1977 (T. H. Pogson), 1 male, 1 female (EMB); Wheeler Co., 9 mi S of Fossil, bark from "slab" of *P. ponderosa*, 18 May 1963 (J. H. Wirtz), 1 female (DRM).

Tribe Dactylocheliferini Beier

The tribe Dactylocheliferini (subfamily Cheliferinae) has been well characterized by Hoff (1956, 1958) and is represented in Oregon by one genus.

Dactylochelifer silvestris Hoff

Beier (1932) established the genus and designated *Chelifer latreillei* Leach from Europe as the type species. Hoff (1956, 1964) briefly characterized the genus in English and included it in his key of 1958. Of the approximately 25 now known species, only two, *Dactylochelifer copiosus* Hoff and *D. silvestris* Hoff, have been reported from the United States. The western species, *D. silvestris*, was described in reasonable detail by Hoff (1956, 1961) and reported from several widely scattered localities in New Mexico (Hoff 1956), Colorado (Hoff 1961), Utah (Knowlton 1972) and now is reported for the first time from Oregon. Oregon specimens appear to be very similar to those reported by Hoff except for the very slightly larger pedipalps. The palpal ratios, however, are consistent with those given by Hoff (1961); hence, the species can easily be separated from *D. copiosus*.

Specimens examined.—Oregon; Deschutes Co., 5 mi S, 1 mi E of Bend, leaf litter of *Arctostaphylos patula*, 20 May 1972 (E. M. Benedict), 1 male (EMB), 9 mi S, 7 mi E of Bend, leaf litter of *Pinus ponderosa*, 20 May 1972 (E. M. Benedict), 1 female (EMB); Grant Co., Canyon City, 4 January 1934 (J. Schuh), 1 female (JCC); Harney Co., 2 mi E of Frenchglen (1280 m), leaf litter of *Salix* sp., 30 July 1971 (E. M. Benedict), 2 females (DRM), 1 March 1974 (E. M. Benedict), 1 female, 2 nymphs (EMB), 23 mi N of Frenchglen (1280 m), leaf litter of *Artemisia tridentata* Nutt., 31 December 1977 (E. H. Gruber and E. M. Benedict), 3 males, 4 nymphs (EMB).

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University of Washington, by William B. Muchmore (WBM) of the University of Rochester, and by Robert O. Schuster (ROS) of the University of California, Davis. The holotype and allotype of the new species are deposited in the American Museum of Natural History (AMNH); paratypes and other specimens are retained in the combined Benedict-Chamberlin-Malcolm Collection (EMB, JCC and DRM), currently housed at Pacific University.

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A STUDY OF THE SPIDERS *DIPOENA ALTA* KEYSERLING, *D. LINEATIPES* BRYANT AND A NEW SPECIES *D. JAMESI* (ARANEAE: THERIDIIDAE)

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ABSTRACT

A study of all the specimens of "*Dipoena alta* Keyserling" in the Museum of Comparative Zoology, Harvard University and the American Museum of Natural History, New York, reveals that *D. alta* probably comprises several species. *Dipoena lineatipes* Bryant is reestablished as a valid species, and a new species, *Dipoena jamesi*, is described. The numerous variations occurring in the three species are illustrated. Detailed cross-reference between the distribution records and the illustrated variations is given. This should facilitate future work on the further division of "*D. alta*" into separate species when additional material becomes available.

INTRODUCTION

During work on spiders from the Indian Ocean atoll of Aldabra, a species of *Dipoena* was discovered which appeared very close to *D. lineatipes* Bryant, as figured by Levi (1953, figs. 11-15, 120-121). Levi (1963) subsequently considered *D. lineatipes* to be a synonym of *D. alta* Keyserling, along with *Euryopsis lutea* Keyserling and *D. pallida* Chickering. (*D. pallida* Chickering, 1943, subsequently became *D. furtiva* Chickering in Roewer, 1951, as the name was preoccupied by *D. pallida* Emerton, 1913.)

It should be noted here that Keyserling's (1886) type specimen of the male *D. alta* was from Montaña de Nancho, Peru and was deposited in the Polish Academy of Sciences, Warsaw (PAS). Levi (1963) examined this specimen and synonymized it with *E. lutea* and the *D. alta* in the British Museum (Natural History) (BMNH), but I was quite unable to obtain it for study. Keyserling also deposited material in BMNH and the male specimen examined here was from Serra Vermella, Brazil. It is possible that both Levi and Keyserling were wrong in synonymizing the *D. alta* from Peru (PAS) with the specimens of "*D. alta*" (and *E. lutea*) from Brazil (BMNH). If this were so, then the BMNH specimens and some of the others which are referred to as "*D. alta* Keyserling" in this paper, would be correctly named "*D. lutea* (Keyserling)". The two male spiders which I examined from Peru (AMNH - see end of "Records" section) were quite different from all the others described and illustrated in this paper, and if the foregoing remarks are found

to be correct, these may prove to be the true "*D. alta*". Although somewhat irritating, this uncertainty makes little difference to the present paper which shows that "*D. alta*" probably comprises several species which will require further study in any case.

The types of *D. alta* and *E. lutea* in BMNH were examined, and a single vial containing "*D. alta*," collected from the Panama Canal Zone, was borrowed from the Museum of Comparative Zoology, Harvard University (MCZ). It was apparent, however, that the MCZ vial contained two distinct species—*D. alta* and *D. lineatipes*.

The species from Aldabra, which initiated this work, appears to be new to science and will be described in another paper in preparation.

In order to establish the degree of variation between individual specimens from the same locality, as well as any geographical variations, it was necessary to examine as many specimens as possible of both species. Accordingly, all specimens of *D. alta* and *D. lineatipes* in both MCZ and the American Museum of Natural History (AMNH), and the type of *D. lineatipes* were borrowed for study.

Preliminary checking through the collections confirmed that *D. alta* and *D. lineatipes* are quite separate species, despite both showing considerable individual variation in somatic and genitalic structure.

It was obvious at this stage that in order to demonstrate effectively the differences between the species, it would be necessary to illustrate fairly profusely.

D. alta shows much more individual variation than *D. lineatipes*. A great deal of variation may be seen in specimens collected together. On the other hand, some specimens from widely separated geographical areas appear identical.

One new species, close to *D. lineatipes*, was found in the collections from Jamaica and Panama and is described here.

These spiders seem so far to have been rather rarely collected, and the answers to many of the questions raised in this paper must await the collection of further material. It is hoped, however, that as well as being a permanent record of the specimens in MCZ and AMNH, this work will provide a reasonable basis for (and a stimulus for) further study.

METHODS

All the drawings of spiders, palpi and epigynes were made to the same scale, precisely, as indicated for figures 1 to 6.

For the purpose of making the drawings, it was so arranged that the author was unaware of the place of origin of each specimen as it was being drawn. It was felt that an accurate drawing could best be made without knowledge of collection data possibly having an influence on the subjective interpretation of structure.

The vials were worked through, and a drawing was made in each case if the specimen did not closely resemble drawings already made. At the end of this, all the drawings were compared. Finally, the drawings were checked against the data in the vials and all the specimens were worked through again, in order to test the opinions arrived at.

Female genitalia were cleared by taking the specimen through to 100% ethanol and then immersing in clove oil. The details of seminal receptacles and ducts were very easily seen in all specimens so treated.

Care was taken to ensure that all epigynes and palpi were drawn from the same viewpoint. The male palpi of *Dipoena* species are frequently held in a rotated position, so

that the ventral aspect faces ectally, and this should be taken into account when comparing the drawings with actual specimens. The left male palpus is figured in each case.

For convenient reference all the illustrations have been grouped together at the end of the work.

Dipoena alta Keyserling
Figs. 1-57, 107, 111-114

Dipoena alta Keyserling, 1886: 45, pl. 12, fig. 159. The male type from Montaña de Nancho, Peru, in PAS was unobtainable for study, and Keyserling's male from Serra Vermella, Brazil (BMNH) is illustrated here (see Introduction, para. 2)

Euryopsis lutea Keyserling, 1891: 227, pl. 9, fig. 168. Female type from Serra Vermella, Brazil. BMNH.

The types of *D. alta* and *E. lutea* are illustrated by Figures 1-6.

Description (male from Panama Canal Zone, Summit. August 1950. Coll. Chickering).—Carapace as in Figs. 34, 37, 40 and 41 and identical with that of the type (Fig. 6). Color orange. Sternum orange. Legs orange and devoid of markings. Abdomen somewhat pointed posteriorly and with a scutum. Color of abdomen pale yellowish; scutum orange. Sooty markings as illustrated and black markings present on each side of spinnerets. Total length 1.68mm. Carapace length 0.84mm; width 0.70mm; height 0.66mm.

Leg measurements (in mm):

	Femur	Tibia + Patella	Metatarsus	tarsus
I	0.60	0.68	0.34	0.24
II	0.50	0.66	0.30	0.24
III	0.54	0.54	0.28	0.22
IV	0.74	0.86	0.40	0.33

Male palp as in Figs. 35-36, 38, 39.

Females from the same locality have similar coloration to males and the general appearance is as in Fig. 7. Female epigyne and genitalia Figs. 8-9.

Variation in females.—Figures 7-21 are of specimens from various localities in Panama Canal Zone, and show considerable size differences. The larger females (Figs. 7-9) were present in collections from Summit as well as from Barro Colorado Island, and might represent a separate species. Specimens from the Forest Reserve were found to be quite markedly smaller (Figs. 16-18) and the epigynes of some specimens from the Experimental Gardens have the connecting ducts widely separated where they meet the sclerotized spot (Figs. 19-21).

Brazilian specimens seem to fall into two groups; those which are close to specimens from Panama Canal Zone (Figs. 22-24), and a rather distinctive form with a yellow abdomen, clearly marked with black, and genitalia which differ in the way the connecting ducts curve around to join the first seminal receptacles (Figs. 25-27). It may be a separate species.

Specimens from Trinidad (Figs. 28-33) show slight differences in general appearance and the genitalia seem close to those of the smaller females from Panama Canal Zone (Figs 10-15). Females from Ecuador have a similar appearance.

Variation in males.—The two males in Figs. 34-39 were collected together from Panama Canal Zone, Barro Colorado Island, and illustrate what could be male dimorphism. (Prof. H. W. Levi comments that the differences between the two male forms could be due to one having had one more moult to become adult than the other.) These two forms occur frequently together and no intermediates were seen. The larger form (Figs. 34-36, 40, 41, 113, 114) has the scutum covering practically the whole of the dorsal abdomen and has a generally robust appearance. The palpi are of a fairly constant size and conformation, and the conductor, radix and embolus tip show little variation in specimens of this particular form. The smaller form (Figs. 37-39, 111, 112) has the scutum covering only the anterior part of the dorsal abdomen and appears slightly less robust in general. The palpi in specimens of this smaller form also are of fairly constant size and conformation, and differ from those of the large form principally in the form of the conductor, radix and embolus tip, and in being slightly smaller. It is this smaller form which is identical to the male type of *D. alta* (Figs. 1, 2, 6).

As already stated, specimens of these two male forms occur together and are distinct in somatic and palpal structure, without intermediates occurring. It has already been noted that the females from the same locality also show some variation in size and genitalic structure and it seems possible that there are two distinct species. One could match the males and females and suggest that Figs. 7-9 (females) and 34-36 (males) represent one species, and Figs. 10-15 (females) and 37-39 (males) represent a separate species—the true *D. alta* (or *D. lutea* if Keyserling and Levi were wrong with the Peruvian type).

If one turns to the males from the Experimental Gardens, Panama Canal Zone (Figs. 42-45) it can be seen that these specimens are smaller still. The abdominal scutum is less distinct, the palpi are smaller and the conductor, radix and embolus tip differ from the previous two forms. Again, no intermediates were seen. Specimens exactly like these were also found from the Forest Reserve, Panama Canal Zone, and one could therefore match these males with the females in Figs. 16-18 and possibly create another distinct species.

Similarly, the Brazilian males were seen to occur in two distinct forms. Although the large form (Figs. 46-48, 52-54) appears to be somewhat variable itself, it differs quite markedly from the small form (Figs. 49-51) and again, these males could perhaps be matched with the females in Figs. 22-27 to give another two species.

The Trinidadian males (Figs. 55-57) appear close to the Panama Canal Zone males in Figs. 37-39.

In this group of spiders one would expect to be able to distinguish between the males of closely related species far more readily than the females. It is the author's view that the differences between the various males described here are not due to male dimorphism; nor are they a reflection of simple individual or geographic variation. It is also likely that the slight differences between the various females are of significance, and are related to those seen in males. Future investigation, when sufficient additional material has been collected, will almost certainly confirm that *D. alta* comprises several distinct species.

Dipoena lineatipes Bryant

Figs. 58-87, 108-110

Dipoena Lineatipes Bryant, 1933: 174, fig. 7. Female type from Florida, Royal Palm Park, (now Royal Palm Area, Everglades National Park) March 1930. MCZ.

The epigyne and internal genitalia of the female type specimen are illustrated by Figs. 58-59. The specimen is in rather poor condition, but the leg markings are clearly visible.

Descriptions (specimens from Panama Canal Zone, Summit, 1950. Coll. Chickering).—Carapace (Figs. 60-62) orange; slightly darker on head in both sexes and thickly suffused with black around the anterior eyes. Sternum yellow-orange with faint sooty markings around margin. Legs yellow-orange with distinct sooty markings in the form of a line running dorsally along the length of the tibiae and metatarsi. These markings, which are very useful diagnostically, are usually most marked on the fourth tibiae, and sometimes reduced on leg III. The leg markings are present in both sexes. Abdomen grey to black, but with posterior end, above the spinnerets, paler in color - even pale yellow in some specimens. The male has a dorsal scutum which is orange-brown in color. Ventrally, abdomen paler, with faint darkening lateral to spinnerets. Total length of female 1.7mm; carapace 0.62mm. Total length of male 1.32mm; carapace 0.64mm long, 0.60mm wide and 0.48mm high. Leg measurements:

Male:

	Femur	Tibia + patella	Metatarsus	tarsus
I	0.52	0.60	0.34	0.24
II	0.46	0.53	0.30	0.23
III	0.50	0.52	0.26	0.24
IV	0.64	0.74	0.36	0.27

Female:

	Femur	Tibia + patella	Metatarsus	tarsus
I	0.56	0.57	0.34	0.24
II	0.52	0.58	0.32	0.23
III	0.51	0.56	0.27	0.23
IV	0.70	0.80	0.38	0.30

Female genitalia Figs. 64-65, 76-77. Male palpus Figs. 85-86.

This species shows much less variation than *D. alta*. The linear markings on the legs were present in all specimens examined, for all locations, despite the fact that many had been in spirit for over forty years.

Variation in females.—The epigynes of females from Panama Canal Zone were, in general, as in Figs. 64, 65, 76, 77, although occasional Florida specimens (Figs. 70-71) were seen to be almost identical. The majority of Florida specimens appeared as in Figs. 58, 59, 67, 68. Some specimens resembling these were also seen from Panama Canal Zone. One specimen from Brazil (Figs. 78-80) was found to be practically identical to the usual Florida form in Figs. 67-68. The specimens from North Carolina (Figs. 72-74), as well as being slightly smaller, differ from all other examples of this species in the way that the connecting ducts curve around to join the first pair of seminal receptacles.

Variation in males.—Males seemed to vary very little in either somatic structure or size. The palpi (Figs. 82, 83, 85-87, 109 110) show slight variation in both the course of the ducts and in the conductor and radix, but this variation occurs just as much in specimens

from the same area as in specimens from different localities, and various intermediate combinations of palpal structure also occur. The palpi are, however, constant in size.

Dipoena jamesi, new species

Figs. 88-106, 115, 116

This species is named after Mr. H. I. James, botanist and formerly biology master at the Dixie Grammar School, Market Bosworth, England.

Description of holotype female.—From British West Indies, Jamaica; Blue Mountains, Hardwar Gap. November 1957. Coll. A. M. Chickering. Deposited in M.C.Z.

Carapace deep orange with sooty markings on cephalic part and black around the anterior eyes. Sternum yellow-orange with faint sooty margin. Abdomen yellowish-grey with dark grey to black markings as illustrated. The darker areas extend around the sides. Ventrally, pale yellowish-grey. Legs orange-brown; femora and tibiae I and II suffused with dark brown. Total length 1.56mm; carapace 0.62mm. Leg measurements:

	Femur	Tibia + patella	Metatarsus	tarsus
I	0.65	0.66	0.36	0.24
II	0.60	0.66	0.34	0.24
III	0.56	0.56	0.30	0.24
IV	0.74	0.90	0.43	0.30

Female epigyne and genitalia figs. 89-90.

Description of allotype male.—Collected with the holotype female. Carapace deep orange with cephalic region darker and black markings around the anterior eyes. Sternum as in female. Abdomen colored as the female, but with a pale orange scutum in addition. Legs orange-brown; tibiae and patellae I and II suffused with dark brown ventrally. Total length 1.38mm. Carapace 0.62mm long, 0.58mm wide and 0.50mm high. Leg measurements:

	Femur	Tibia + patella	Metatarsus	tarsus
I	0.60	0.62	0.34	0.22
II	0.54	0.64	0.30	0.22
III	0.53	0.54	0.30	0.23
IV	0.66	0.78	0.36	0.30

Male palpus Figs. 101, 102.

Eight male and seven female paratypes were collected with the types.

Variation.—Little variation in the size or coloration of either sex was observed. The female from Panama, El Volcán (Figs. 97-99) differs no more from the Jamaican specimens than the latter do from one another. No males were found in the collections from Panama, but the Jamaican males showed only slight variation in palpal structure.

Dipoena furtiva Chickering

Dipoena pallida Chickering, 1943: 364, figs. 50, 51. Female holotype from Barro Colorado Island, Panama Canal Zone. MCZ. Preoccupied by *Dipoena pallida* Emerton (1913).

Dipoena furtiva Chickering in Roewer, 1951: 455. New name for *D. pallida* Chickering, 1943 (preoccupied); Levi, 1953: 3, fig. 18 (female).

Levi's 1953 figures of *D. furtiva* genitalia appear to be those of *D. alta*. Two vials borrowed from MCZ were labelled as "*Dipoena pallida* sp. nov. paratype female" and in each was a second label "*D. furtiva* Chick." One specimen, from Porto Bello, appears close to *D. barro* Levi, and the other, from Fort Davis, is a specimen of *D. alta* similar to Figs. 10-15.

COMPARATIVE DESCRIPTIONS OF *D. ALTA*, *D. LINEATIPES* AND *D. JAMESI*

Figures 107-116 explain the terms used in the discussion of the genitalia.

In general, the drawings in this paper should make future identification of specimens easy. *D. alta* may comprise several species.

Both sexes of *D. lineatipes* may be easily distinguished from *D. alta* and *D. jamesi* by the linear sooty markings on the dorsal aspect of the legs. This feature seems, perhaps surprisingly, to be reliable and to withstand long preservation. Some *D. alta*, particularly smaller specimens, may have appreciable darkening of the tibiae, but this is never in the form of a dorsal line. *D. jamesi* frequently has sooty markings on the legs which sometimes take the form of a line on the ventral, but not the dorsal aspect of the legs.

The female genitalia of *D. lineatipes* and *D. jamesi* appear, especially when cleared, to have the sclerotized spot ("X" in Fig. 108) separate from the external openings of the connecting ducts, and the line of separation seems to extend laterally for a short distance. No such division of the structure is seen in *D. alta* genitalia. The posterior lip of the epigyne tends to be thinner and closer to the epigastric fold in *D. lineatipes* and *D. jamesi* than in *D. alta*. The way in which the connecting ducts curve backwards from their most anterior point to join the first pair of seminal receptacles was at first thought to be of significance. In *D. alta* they curve inwards, in *D. lineatipes* outwards, and in *D. jamesi* they take an intermediate course. However, exceptions to this can be seen in Fig. 27 (for *D. alta*) and in Fig. 74 (for *D. lineatipes*). This feature might be of use in future work on *D. alta*. The female genitalia of *D. jamesi* differ from those of *D. lineatipes* not only in the course of the ducts, but also in the fact that the first pair of seminal receptacles are *spherical and relatively smaller*.

The shape and markings of the carapace are useful in separating the males of the three species, and even small specimens of *D. alta* (e.g. Figs. 42-43) can be distinguished from *D. lineatipes* and *D. jamesi*. When the male carapace of *D. alta* is viewed laterally, (Figs. 41, 43) the clypeus is more or less straight and is parallel to the slope posteriorly, irrespective of the overall size of the spider. In both *D. lineatipes* (Fig. 61) and *D. jamesi* (Fig. 104), the clypeus appears slightly concave when viewed laterally, and the lines representing the clypeus and posterior border converge if produced dorsally, especially in *D. jamesi*. It is difficult to put into words the differences between the male carapaces of *D. lineatipes* and *D. jamesi* as seen from a dorsal view. However, Figs. 81, 84 and Figs. 100, 103 will be found surprisingly useful when it comes to comparing them with specimens. The small black mark lying in the "bottom" of the "U" (anterior to the longitudinal line) is only present in *D. jamesi*.

The male palpi of *D. alta* are easily distinguished from those of *D. lineatipes* and *D. jamesi* by reference to the illustrations, and nearly always by their greater size. The palpi of *D. jamesi* are most easily distinguished from those of *D. lineatipes* and *D. alta* by the large notch in the subtegulum - "N" in Fig. 116. Also the radix in *D. jamesi* has a spatulate tip, whereas in *D. lineatipes* it is pointed. The tip of the embolus is often visible in *D. alta* specimens, but not usually in *D. lineatipes*. In *D. jamesi* the embolus tip was quite prominent in all specimens seen.

RECORDS

The following is a complete list of the specimens examined from MCZ and AMNH and for each is given the locality, date, collector, museum and the name of the species in the vial. In addition, reference to the illustrations in this paper is given - eg. "female Figs. 7 - 9," where the specimen was the actual one drawn, or "2 females as figs. 7 - 9" where the specimens in the vial closely resemble the figures. It was felt that this would be of greater potential value to further study, especially of the *D. alta* variants, than a distribution map. The information is put into paragraph to save expense and is arranged roughly from North (U.S.A.) to South (Brazil).

U.S.A.: **NORTH CAROLINA**: Beaufort; Lennox Point, AMNH, *lineatipes* female Figs. 72 - 74. **ALABAMA**: Baldwin Co., Jackson Oak: Jan. 1941, Archer, AMNH, *lineatipes* female as figs. 66 - 68; Baldwin Co., Gasque: June 1950, Archer, AMNH, *lineatipes* female as figs. 66 - 68. **TEXAS**: Houston: June 1936, Mulaik, AMNH, *lineatipes* male as figs. 81 - 83. **LOUISIANA**: Greenburg: March 1936, AMNH, *lineatipes* female as figs. 66 - 68. **FLORIDA**: Alachua Co.: Nov. 1939, AMNH, *lineatipes* female as figs. 66 - 71 & males as figs. 81 - 87. Glades County, Fish Eating Creek: Feb. 1951, Nadler, AMNH, *lineatipes* female as figs. 66 - 68. Highlands Hammock, State Park: Feb. 1951 Nadler, AMNH, *lineatipes* male Fig. 87. Lake Istokpoga (3 - 5 miles South of): Dec. 1950, Nadler, AMNH, *lineatipes* female as figs. 66 - 68; Feb. 1951, Nadler, AMNH, *lineatipes* females as figs. 66 - 71 & males as figs. 81 - 83. Lake Placid, Archbold Biol. Sta.: Feb. 1951, Nadler, AMNH, *lineatipes* male as figs. 81 - 83. Kendall: Dec. 1950, Nadler, AMNH, *lineatipes* female as figs. 66 - 68 & male as figs. 84 - 86; Jan 1951, Nadler, AMNH, *lineatipes* male as figs. 84 - 86 & male as figs. 81 - 83; Feb. 1951, Nadler, AMNH, *lineatipes* female as figs. 66 - 68 & male as figs. 81 - 83; Nov. 1952, Nadler, AMNH, *lineatipes* male as figs. 81 - 83 & male as figs. 84 - 86; Nov. 1952, Nadler, AMNH, *lineatipes* females Figs. 66 - 71 and as figs. 62 - 65 & 75 - 80, & male Figs. 81 - 83 and as figs. 84 - 87; Mar. 1953, Nadler, AMNH, *lineatipes* female as figs. 66 - 71; Mar. 1953, Nadler, AMNH, *lineatipes* male as figs. 81 - 83; Mar. 1953, Nadler, AMNH, *lineatipes* females as figs. 66 - 71 & males as figs. 81 - 83. Myakka River, State Park: Dec. 1963, Ivie, AMNH, *lineatipes* male as figs. 81 - 83. Sarasota: Dec. 1950, Nadler, AMNH, *lineatipes* females as figs. 66 - 71 & 78 - 80. **JAMAICA**: Blue Mts., Hardwar Gap: Nov. 1957, Chick., MCZ, *jamesi*, 8 females Figs. 88 - 93 & 9 males Figs. 100 - 106; June 1958, Sanderson, MCZ, *jamesi* females as figs. 88 - 93; Nov. 1959, Nadler, AMNH, *jamesi* females Figs. 94 - 96. St. Andrews par., Morces Gap: July 1958, Sanderson, MCZ, *jamesi* males as figs. 100 - 102. **TRINIDAD**: Simla: Dec. 1954, Nadler, AMNH, *alta* female Figs. 28 - 30; Dec. 1954, Nadler, AMNH, *alta* male Figs. 55 - 57; April 1964, Chick., MCZ, *alta* females Figs. 31 - 33. **PANAMA**: El Volcán: Aug. 1950, Chick., MCZ, *jamesi* female Figs. 97 - 99. Panama Canal Zone: Barro Colorado Island: July 1939, Chick., MCZ, *alta* female Figs. 13 - 15; July 1939, Chick., MCZ, *alta* female as figs. 7 - 9; June 1950, Chick., MCZ, *alta*, female Figs. 7 - 9; April 1953, Nadler, AMNH, *alta* females as figs. 7 - 12 & males as figs. 34 - 36; July 1954, Chick., MCZ, *alta* female as figs. 7 - 9; July 1954, Chick., MCZ, *alta* male as figs. 34 - 36; July 1954, Chick., MCZ, *alta* males Figs. 34 - 36 & Figs. 37 - 39; July 1954, Chick., MCZ, *alta* males as figs. 34 - 36; Aug. 1954, Chick., MCZ, *alta* male as figs. 37 - 39; Dec. 1957, Chick., MCZ, *alta* male as figs. 34 - 36; Mar. 1958, Chick., MCZ, *alta* female Figs. 10 - 12; May 1964, Chick., MCZ, *alta* female as figs. 13 - 15 & male as figs. 37 - 39. Panama Canal Zone, Experimental Gardens: July 1954, Chick., MCZ, *alta* males Figs. 42 - 45 & male as figs. 37 - 39; July 1955, Chick., MCZ, *alta* female Figs. 19 - 21; July 1955, Chick., MCZ, *alta* male as figs. 34 - 36, 3 males as figs. 42 - 45 & female as figs. 19 - 21; *lineatipes* male as figs. 84 - 86. Panama Canal Zone, Forest Reserve: Dec. 1957, Chick., MCZ, *alta*

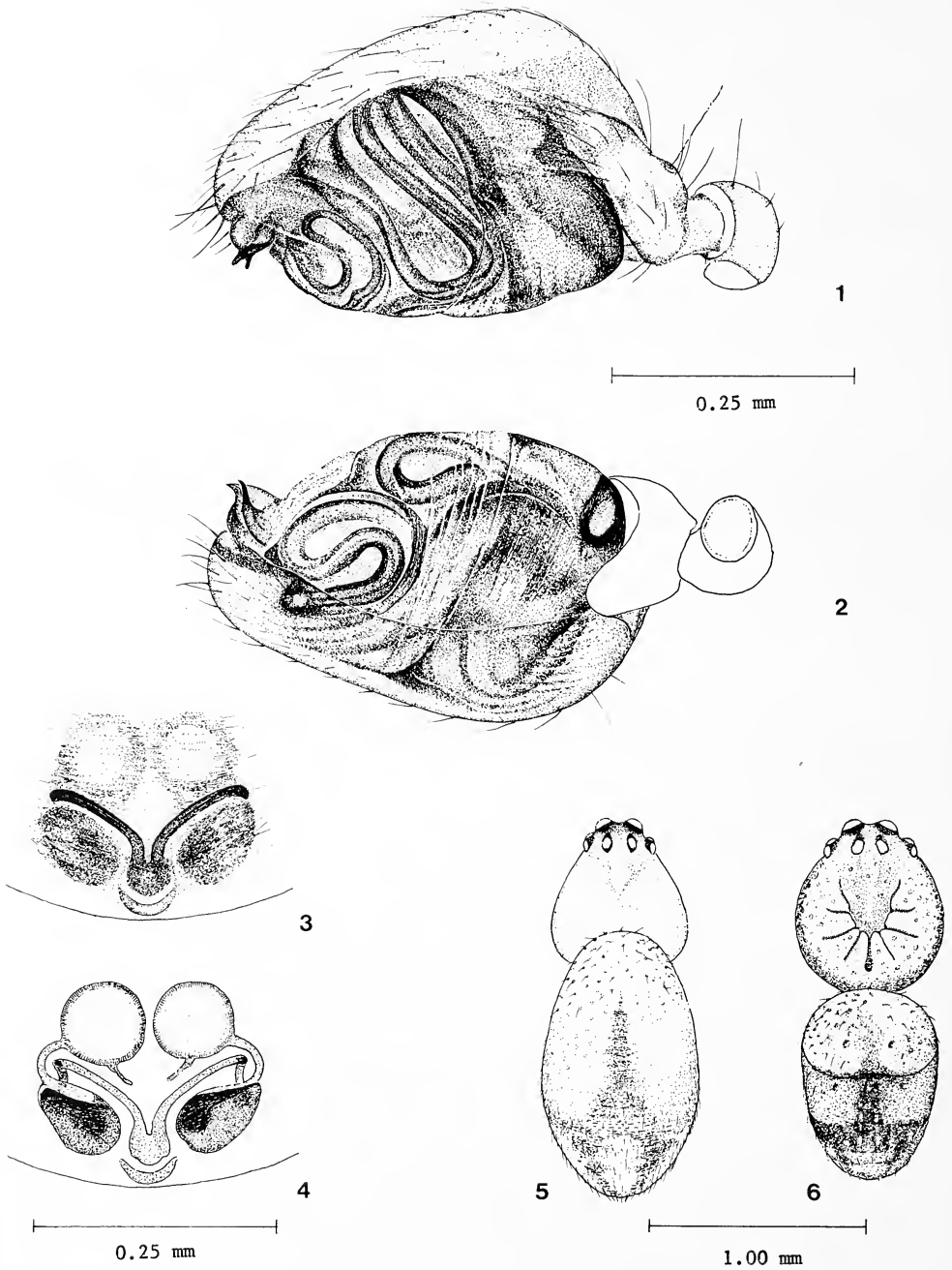
female Figs. 16 - 18 & male as figs. 42 - 45. Panama Canal Zone, Summit: July 1950, Chick., MCZ, *alta* female as figs. 7 - 9; July 1950, Chick., MCZ, *alta* males as figs. 34 - 36; July 1950, Chick., MCZ, *alta* females as figs. 7 - 9; July 1950, Chick., MCZ, *lineatipes* female as figs. 75 - 77; Aug. 1950, Chick., MCZ, *alta* males as figs. 34 - 36 & *lineatipes* female Figs. 75 - 77; Aug. 1950, Chick., MCZ, *alta* males as figs. 34 - 36 and *lineatipes* males & females Figs. 84 - 86 and Figs. 60 - 65. ECUADOR: El Oro: Río Jubones, Pasaje: Oct. 1942, Wells, MCZ, *alta* female as figs. 31 - 33 & males as figs. 37 - 39. BRAZIL: Campo Grande: Jan. 1959, Nadler, AMNH, *alta* male as figs. 52 - 54 except that the abdomen has only a short median mark & lacks the dark areas on each side of the posterior abdomen. Espírito Santo, Santa Teresa: Jan. 1959, Nadler, AMNH, *alta* females Figs. 25 - 27 & males Figs. 46 - 51. Rio de Janeiro, Botanical Gardens: Jan. 1959, Nadler, AMNH, *alta* females Figs. 22 - 24 and *lineatipes* female Figs. 78 - 80. São Paulo, Forest Reservation: Jan. 1959, Nadler, AMNH, *alta* 1 male as figs. 46 - 48 and one intersex, with complete male somatic development, but with rudimentary male palpi and female epigyne; Jan. 1959, Nadler, AMNH, *alta* female as figs. 25 - 27. PANAMA CANAL ZONE: Barro Colorado Island: July 1934, MCZ, female labelled as "*D. alta*" which it is not. It may be *D. barro* Levi. Fort Davis: Aug. 1936, labelled "*Dipoena pallida* sp. nov. paratype female" and "*Dipoena furtiva* Chick." is *alta* female as figs. 10 - 15. Porto Bello: labelled "Aug. 1936, *Dipoena pallida* sp. nov. paratype female" and "*Dipoena furtiva* Chick." is neither *alta* or *lineatipes*. It appears close to *D. barro* Levi. PERU: Divisoria, Dept. of Huanuco: Sept/Oct. 1946; Two vials; F. Woytkowski, AMNH; Contain male spiders in poor condition which are quite different from the species illustrated in this paper. (See "Introduction," paragraph 2.)

ACKNOWLEDGEMENTS

My thanks are due to Prof. H. W. Levi (MCZ), Dr. N. I. Platnick (AMNH) and Mr. F. Wanless (BMNH) for the loan of specimens in their care, and to Prof. Levi and Dr. O. Francke (Texas Tech University) for reading through the manuscript and making helpful suggestions.

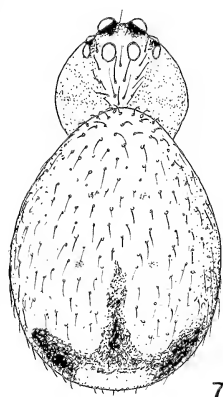
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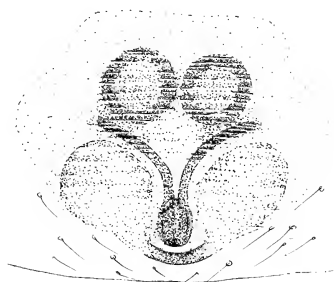


Figs. 1, 2, 6.—*D. alta* male type: 1, palpus, ectal view; 2, palpus mesal view; 6, carapace and abdomen, dorsal view.

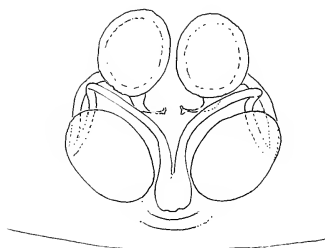
Figs. 3, 4, 5.—*E. lutea* female type: 3, epigyne; 4, female genitalia; 5, carapace and abdomen.



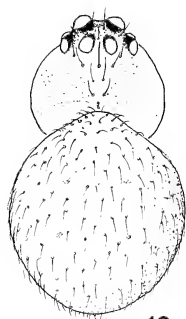
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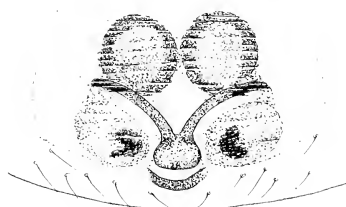
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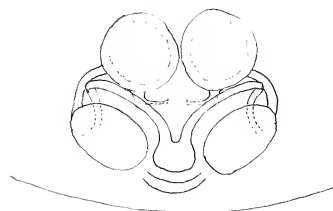
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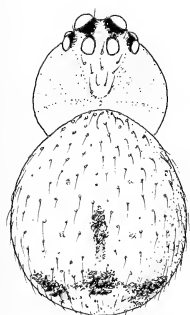
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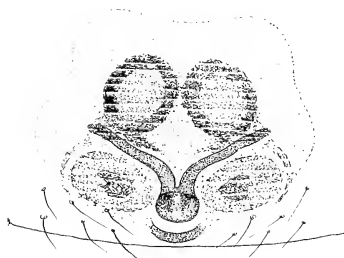
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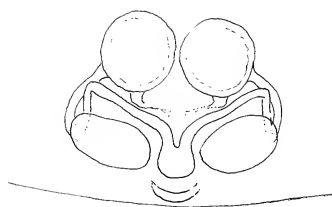
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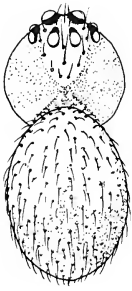


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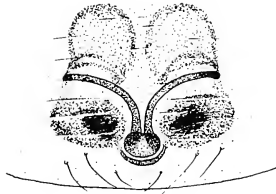


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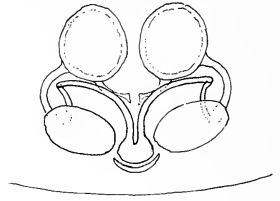
Figs. 7 - 15.—*D. alta* females, epigynes and genitalia from Panama Canal Zone, Barro Colorado Island.



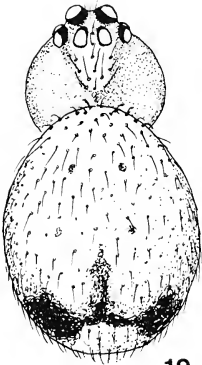
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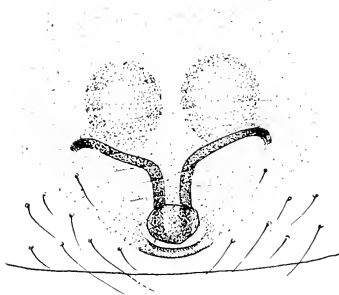
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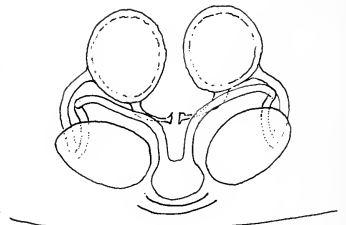
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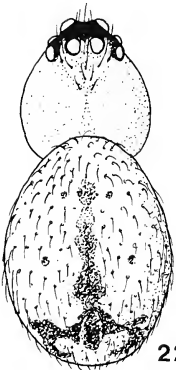
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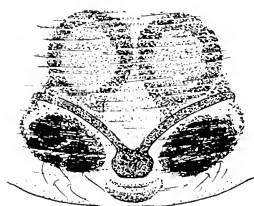
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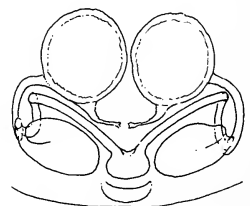
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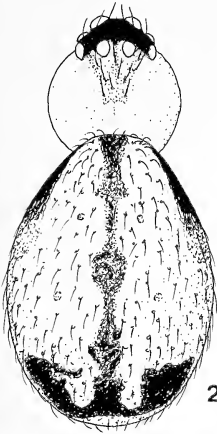


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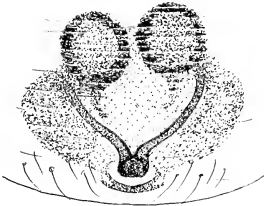


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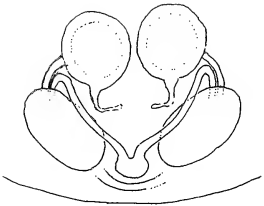
Figs. 16 - 18.—*D. alta* female, epigyne and genitalia from Panama Canal Zone, Forest Reserve. Figs. 19 - 21.—*D. alta* female, epigyne and genitalia from Panama Canal Zone, Experimental Gardens. Figs. 22 - 24.—*D. alta* female, epigyne and genitalia from Brazil, Rio de Janeiro, Botanical Gardens.



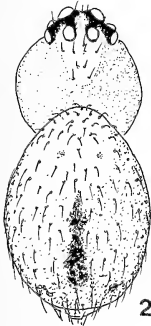
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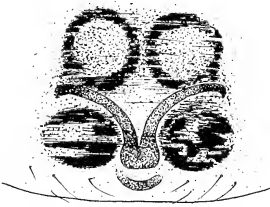
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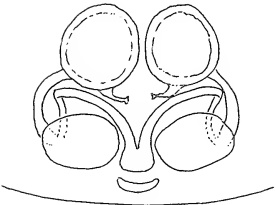
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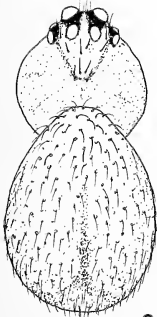
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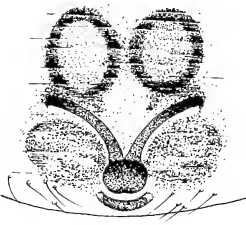
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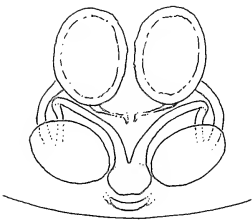
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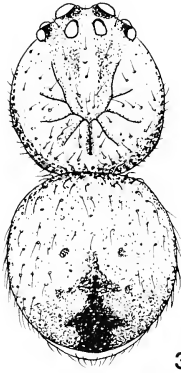


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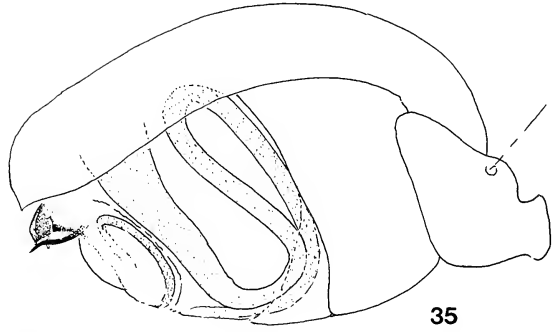


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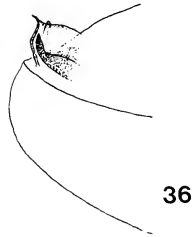
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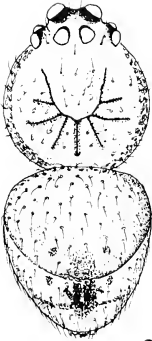
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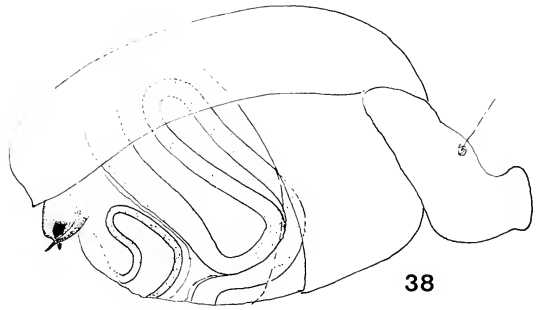
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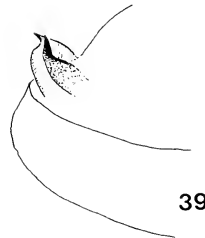
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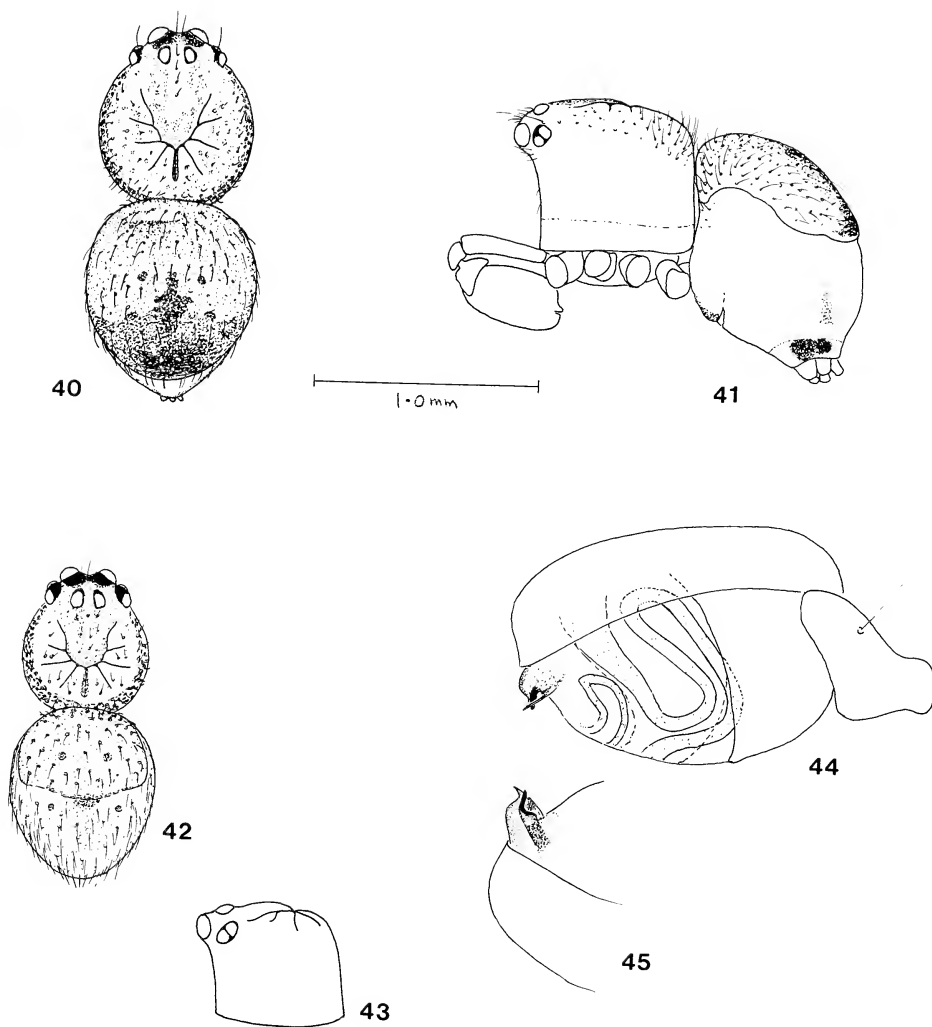


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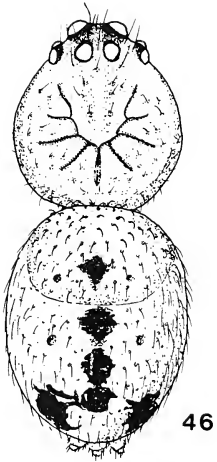


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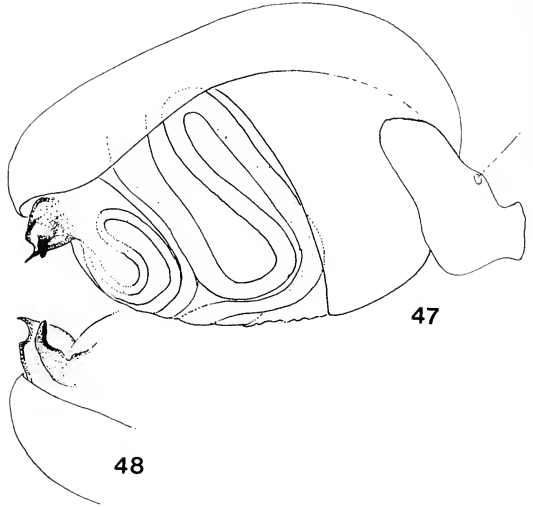
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Figs. 40 - 41.—*D. alta* male (large form) from Panama Canal Zone, Summit: 40, dorsal; 41, lateral view. Figs. 42 - 45.—*D. alta* male from Panama Canal Zone, Experimental Gardens: 42, carapace and abdomen; 43, carapace, lateral view; 44, palpus, ectal view; 45, palpal tip, mesal view.

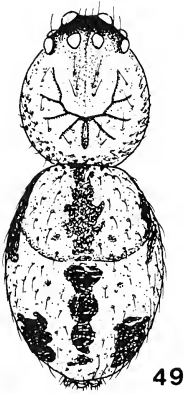


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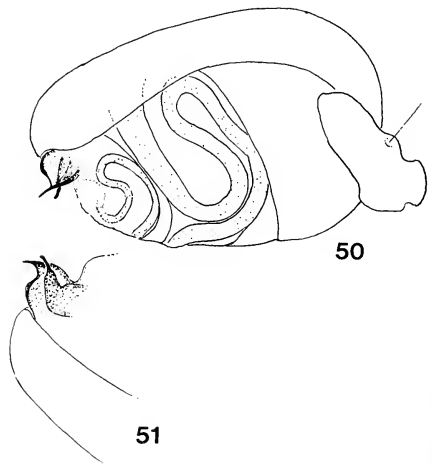


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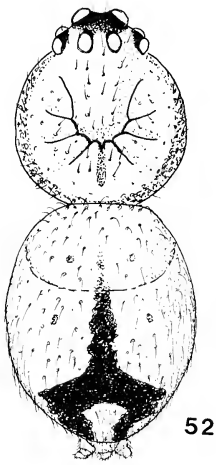
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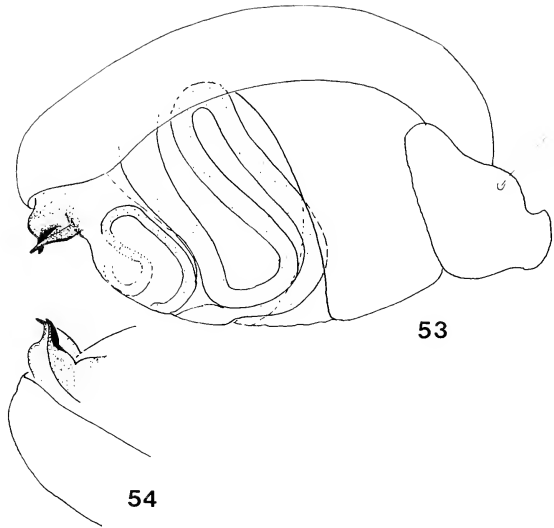
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Figs. 46 - 48.—*D. alta* male (large form) from Brazil, Espírito Santo, Santa Teresa: 46, carapace and abdomen; 47, palp, ectal view; 48 palpal tip, mesal view. Figs. 49 - 51.—*D. alta* male (small form from Brazil, Espírito Santo, Santa Teresa: 49, carapace and abdomen; 50, palp, ectal view; 51, palpal tip, mesal view.

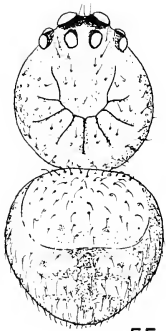


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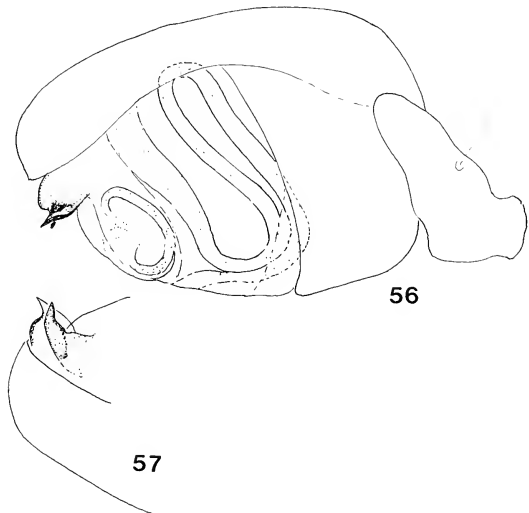


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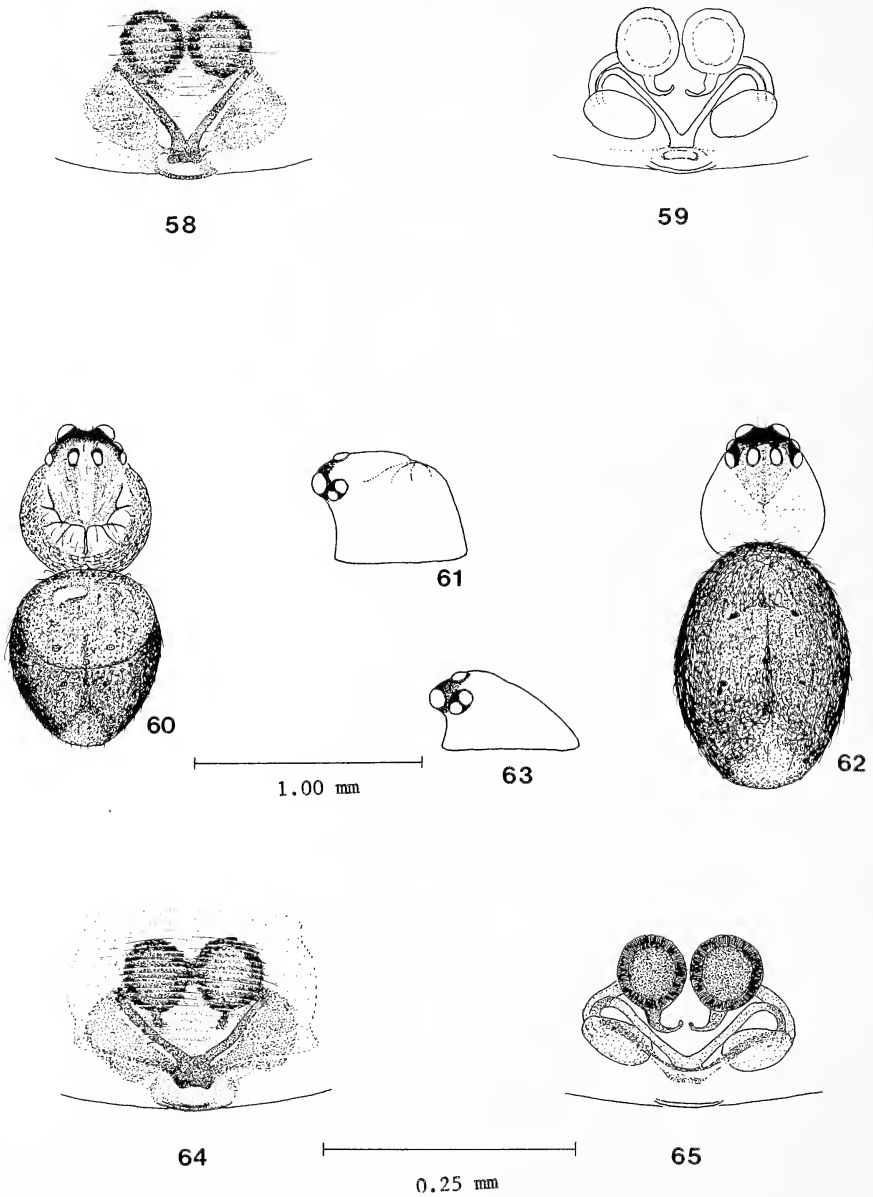
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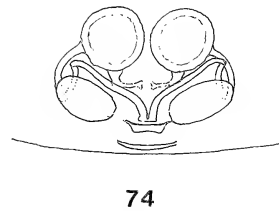
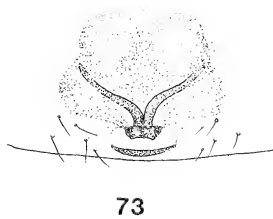
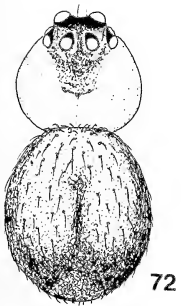
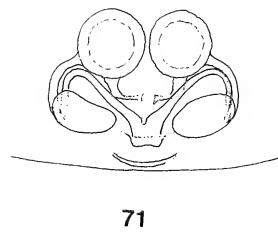
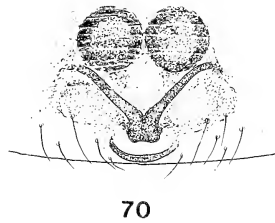
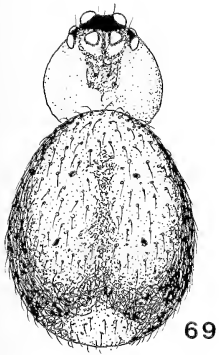
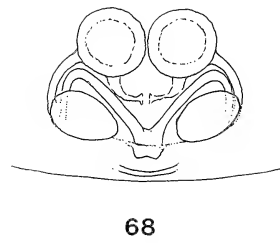
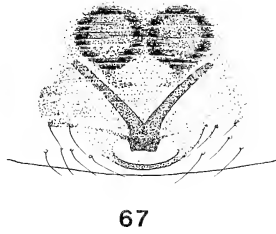
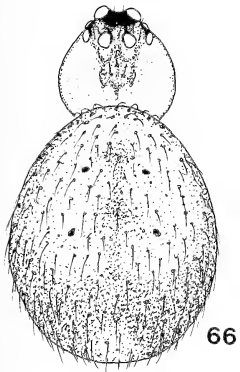
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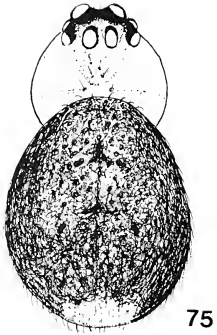
Figs. 52 - 54.—*D. alta* male from Brazil, Rio de Janeiro, Teresopolis: 52, carapace and abdomen; 53, palpus, ectal view; 54, palpal tip, mesal view. Figs. 55 - 57.—*D. alta* male from Trinidad, Simla: 55, carapace and abdomen; 56, palpus, ectal view; 57, palpal tip, mesal view.



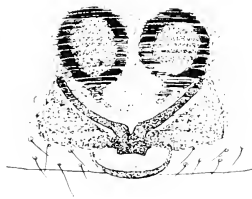
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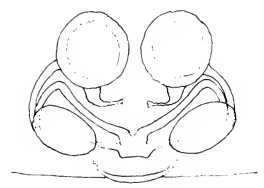
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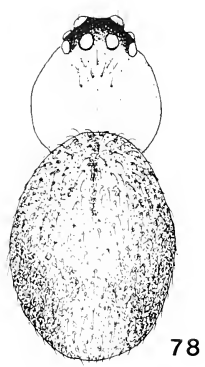
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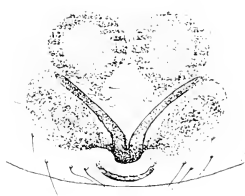
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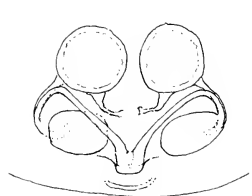
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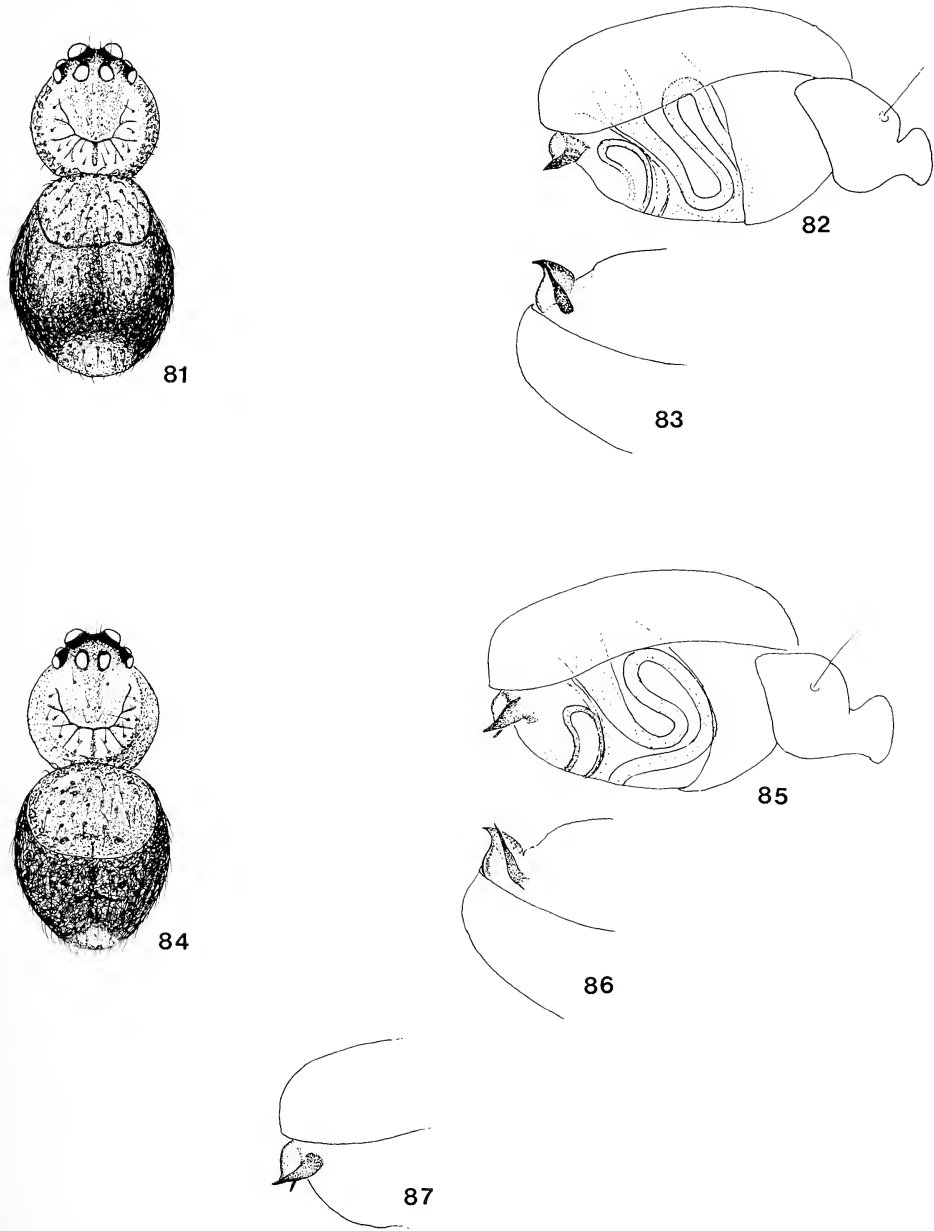


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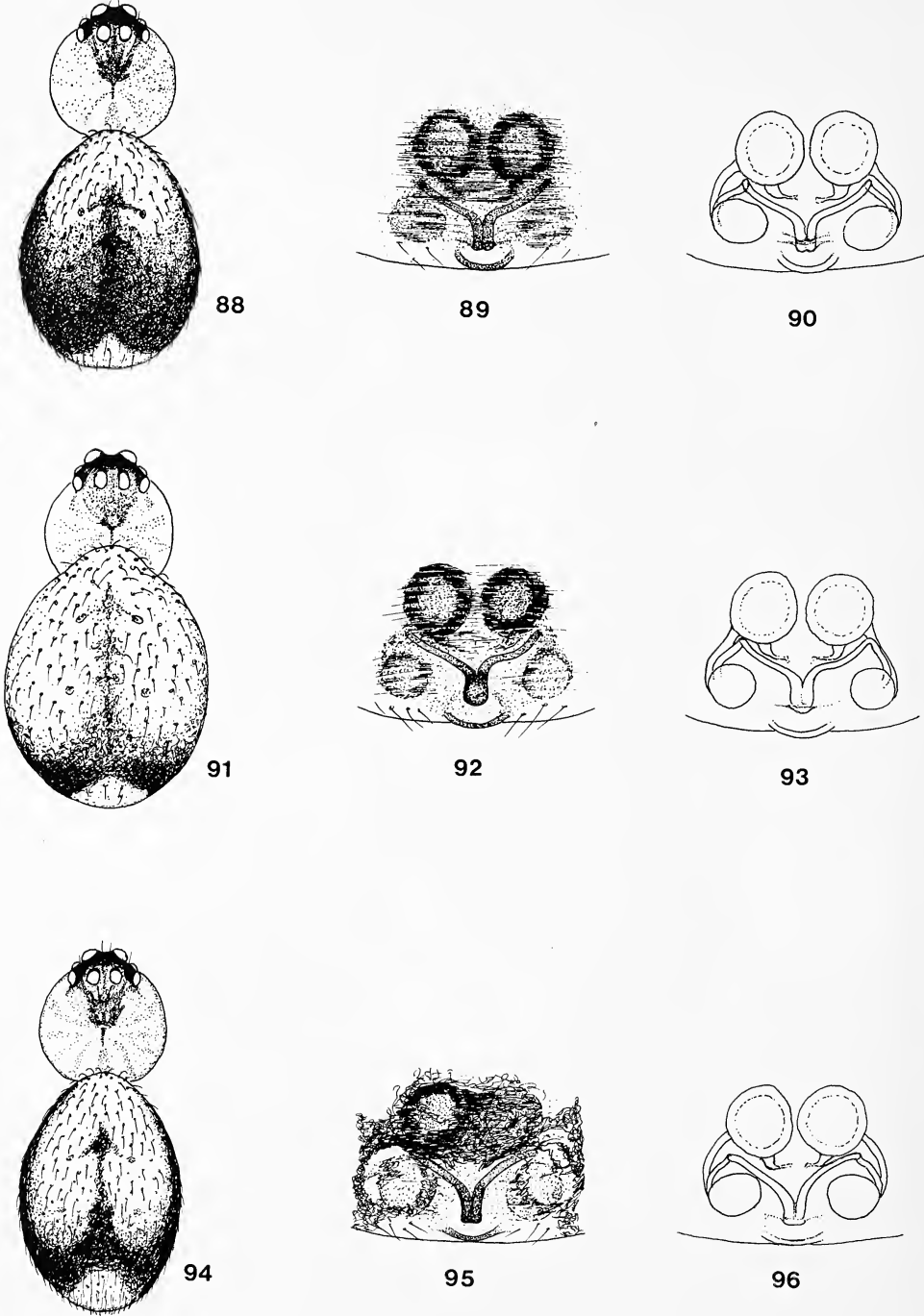


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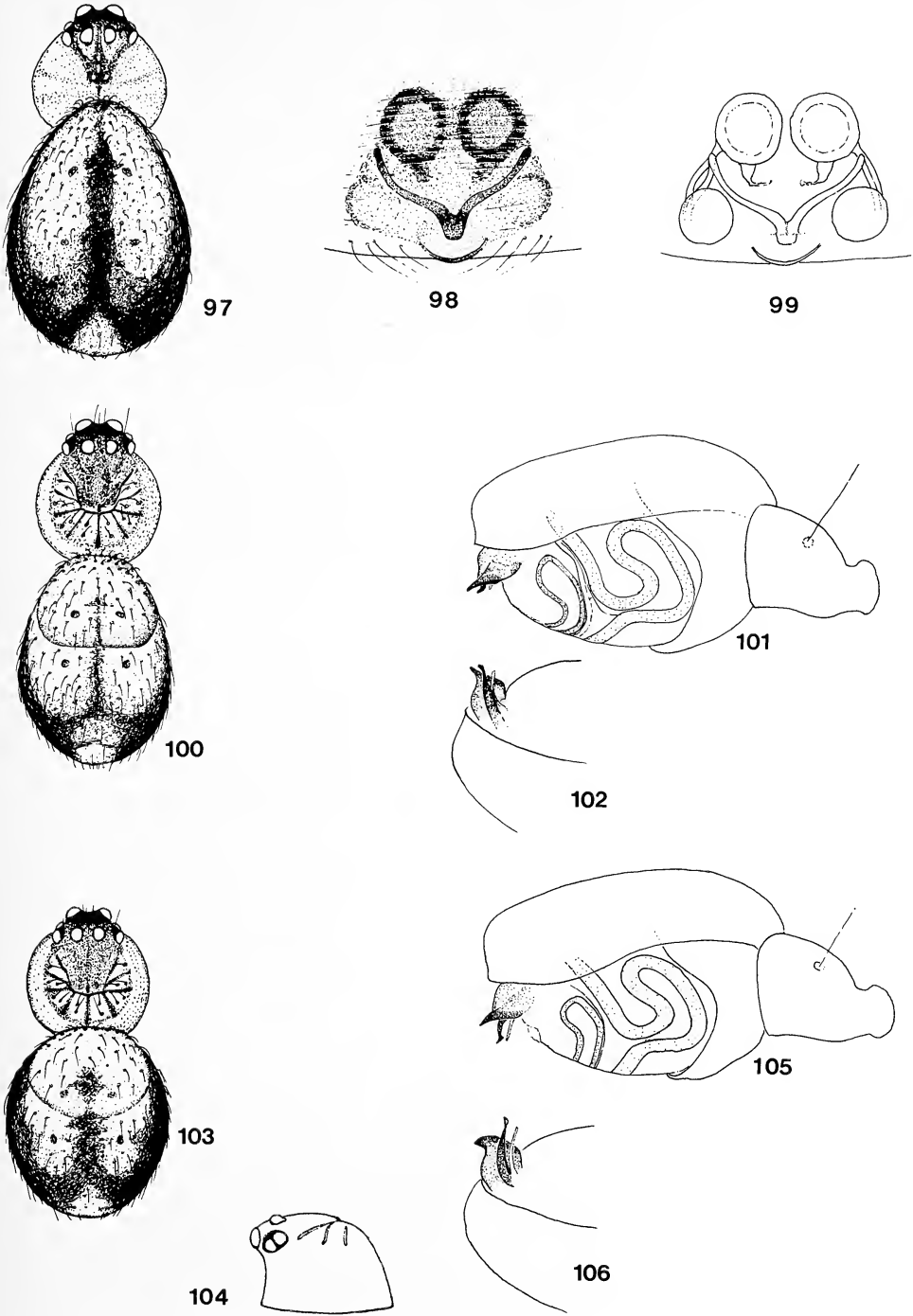
Figs. 75 - 77.—*D. lineatipes* female, epigyne and genitalia, from Panama Canal Zone, Summit. Figs. 78 - 80.—*D. lineatipes* female, epigyne and genitalia, from Brazil, Rio de Janeiro, Botanical Gardens.



Figs. 81 - 83.—*D. lineatipes* male from Florida, Kendall; 81, carapace and abdomen; 82, palpus, ectal view; 83, palpal tip, mesal view. Figs. 84 - 86.—*D. lineatipes* male from Panama Canal Zone, Summit: 84, carapace and abdomen; 85, palpus, ectal view; 86, palpal tip, mesal view. Fig. 87.—*D. lineatipes* male; palpal tip, ectal view; from Florida, Highlands Hammock.



Figs. 88 - 96.—*D. jamesi* females, epigynes and genitalia; from Jamaica, Blue Mountains, Hardwar Gap.



Figs. 97 - 99.—*D. jamesi* female, epigyne and genitalia, from Panama, El Volcán. Figs. 100 - 106.—*D. jamesi* males, from Jamaica, Blue Mountains, Hardwar Gap: 100, 103, carapace and abdomen; 104, carapace, lateral view; 101, 105, palpus, ectal view; 102, 106, palpal tip, mesal view.

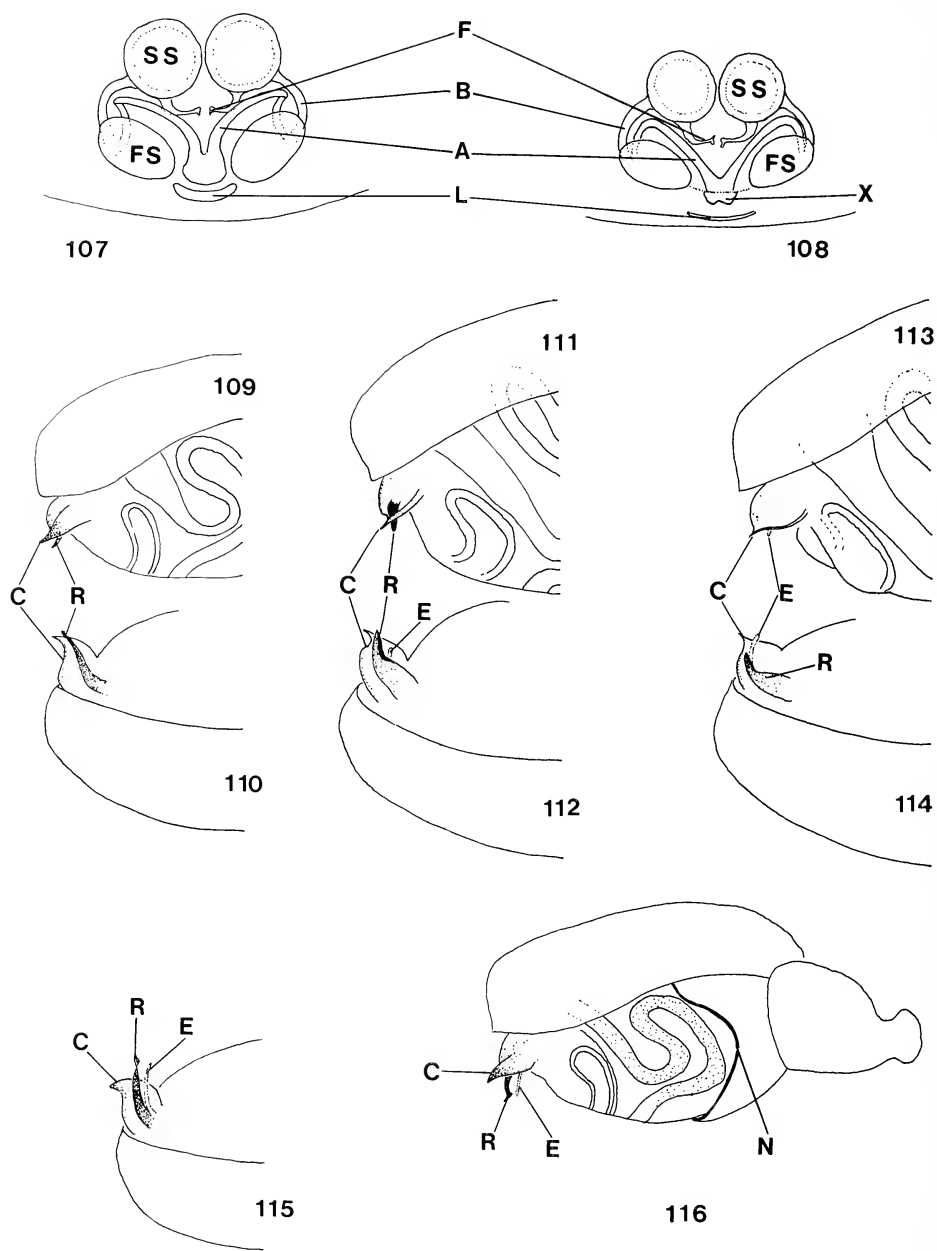


Fig. 107.—*D. alta* female genitalia. Fig. 108.—*D. lineatipes* female genitalia. Figs. 109, 110.—*D. lineatipes* male palpus. Figs. 111, 112.—*D. alta* male palp. Figs. 113, 114.—*D. alta* male palp. Figs. 115, 116.—*D. jamesi* male palp. Abbreviations: A - Connecting canal, B - Canal connecting first and second seminal receptacles, C - Conductor, E - Embolus, F - Fertilization duct, FS - First seminal receptacle, L - Posterior lip of epigyne, N - Notch in subtegulum, R - Radix, SS - Second seminal receptacle, X - See text.

OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY AND LIFE HISTORY OF *MEGACORMUS GERTSCHI* DIAZ (SCORPIONES: CHACTIDAE; MEGACORMINAE)

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ABSTRACT

Four *Megacormus gertschi* Diaz females gave birth in the laboratory to 19, 25, 26 and 75 young. Laboratory-born specimens were raised to the fourth instar, and morphometric analysis of growth rates leads to the prediction that this species attains sexual maturity with the eighth instar. The mating behavior and the spermatophore are described, providing the only observations available for the subfamily Megacorminae.

INTRODUCTION

The chactid subfamily Megacorminae, endemic to México and Guatemala, is represented by two relatively rare genera: *Plesiochactas* Pocock, represented by two poorly known species; and *Megacormus* Karsch, represented by three species, of which only *Megacormus gertschi* Diaz is adequately represented in collections (Soleglad 1976). *M. gertschi* occurs on the eastern slopes of the Sierra Madre Oriental at elevations of 800-2000 m, and has been found in the Mexican states of Tamaulipas, Queretaro, San Luis Potosí, Hidalgo, and Veracruz (Soleglad 1976).

Nine specimens of *M. gertschi*, two adult males, five adult females, and two juveniles were taken near El Madroño (1800 m), Queretaro (27 km west of Xilitla, San Luis Potosí), on 10 March 1977. The specimens were returned to Lubbock, Texas alive, and the following brief observations are the first ever reported on the biology of any member of the subfamily Megacorminae.

MATERIALS AND METHODS

Specimens were kept, and the observations made, in an environmental chamber at $26.6 \pm 1^\circ\text{C}$. Darkness was interrupted only during maintenance activities, which occurred at various hours of the day. Field caught specimens were kept individually in 500 ml wide-mouth jars (85 mm internal diameter), with a 2 cm deep layer of soil and a small rock to provide shelter. Young scorpions born in the laboratory were kept individually in

75 ml wide-mouth jars (50 mm internal diameter), with a 1 cm deep layer of soil and no sheltering objects. Matings were staged in a plastic arena 26 cm in diameter, 9 cm deep, with a single layer of absorbent paper for substrate.

The specimens were checked and watered daily, prey was presented on alternate days. Adults were offered live immature cockroaches, *Nauphoeta cinerea* (Olivier). The rearing and maintenance of hundreds of scorpions in the laboratory over the past five years has led to the development of the following rule-of-thumb regarding "optimal" prey size: the prey should be about as long as the pedipalp chela of the scorpion (optimality in this case refers to the greatest success observed, but not quantified, in prey capture and prey consumption). Scorpions tend to retreat from larger prey, so that the capture rate is low. Smaller prey are readily captured and consumed, but very large numbers are needed if scorpion development is to proceed normally. Immature scorpions, especially the youngest instars, often pose a problem in this respect since most readily available prey items (e.g., small cockroaches, fruit flies, flour beetles) are too large to be taken. Mortality due to starvation in early instars had been very high in many of my studies (including the present one) until a solution was found: young scorpions readily accept dead prey. Cockroaches were cut into small pieces and offered to the young scorpions, which fed on them without having to subdue the prey or pierce its exoskeleton. Baerg (1961) reported that some scorpions accept raw red meat for food. Unconsumed prey remains decompose rapidly and favor the growth of fungi and mites in the rearing containers; this was prevented by the removal of prey remains each day.

The morphometric analysis used to predict the number of instars required to attain sexual maturity has been modified from Francke (1976). Measurements of three structures (carapace length, metasomal segment V length, and pedipalp chela length) were obtained from exuvia or from preserved specimens representing known instars, at 20 X magnification. The growth factor (Dyar's constant) between succeeding instars was determined for each structure on each individual by dividing the dimension at one instar by the dimension at the previous instar. The average growth factor per molt for each structure was then calculated from the pooled data. Predicted dimensions for each structure on life stages not observed were calculated, as 95% Confidence Limits (C. L.), as follows: (a) 95% C. L. were calculated for each structure on the largest observed instar using the formula 'mean \pm $t_{0.05}$ standard deviation'; (b) the upper and lower 95% C. L. for each structure on the largest observed instar were multiplied by the average growth factor of that structure to set the 95% C. L. of predicted dimensions for the following instar; (c) and so forth for dimension predictions on all structures for successive instars.

OBSERVATIONS AND DISCUSSION

Birth behavior.—Four of the five adult females gave birth in the laboratory on 5 and 6 May 1977, 56-57 days after they were captured. The apparent synchrony in births could be due to a number of reasons, among which (a) chance, (b) a highly synchronized mating season, and (c) simultaneous termination of embryonic diapause in the laboratory are distinct possibilities.

Females assume a tilting position to give birth similar to that described for other scorpions. The birth basket receives the first instars and is formed by the first pair of legs (Fig. 1). In *Euscorpius carpathicus* (L.) and *Euscorpius italicus* (Herbst), the only other chactids studied (Angermann 1957), the first two pairs of legs form the birth basket.

One of the females was observed for two hours while giving birth. In that time seven young were born, at an average interval of 17 minutes between births (range 11 to 29 min.). Three of the young emerged head first, and four emerged tail first. Soon after birth the newborns shed their birth membrane while still in the birth basket. While the origin of the birth membrane is not known, it is possible that it represents the partially fused embryonic membranes (serosa and amnion) observed in other apoikogenic scorpions (Johnson 1891). The first instars move anteriorly and pass over the female's chelicerae on their ascent to her dorsum (Figs. 1 and 2). They position themselves at random over the tergites and posterior region of the female's carapace. Similar behavior occurs in *Euscorpium* spp. (Angermann 1957).

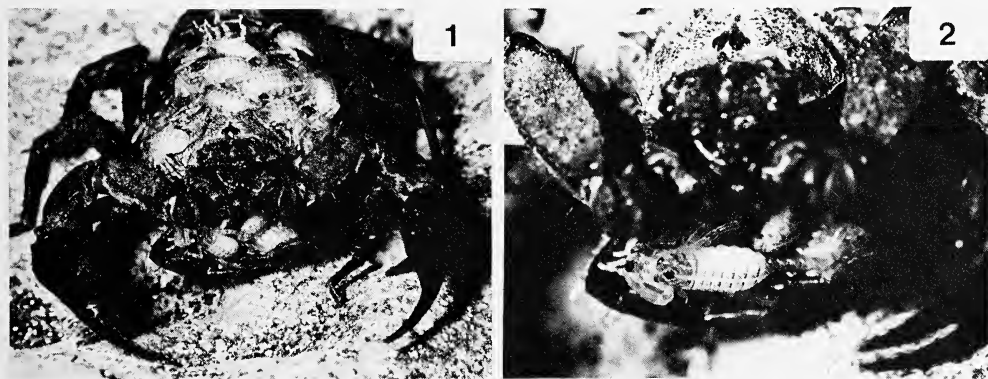
Litter sizes were as follows: 19, 25, 26 and 75 young. The female that had 75 young ranked second in size among the four that gave birth; it died of unknown causes two days after giving birth, and the first instars could not be saved.

Life history.—The data pertain to early instars. This is sufficient, however, to make some predictions on the entire life history of *M. gertschi*.

FIRST INSTAR—The first instars spent 10 to 12 days on the female's dorsum prior to molting. In *Euscorpium* spp. this stage lasts six to ten days (Angermann 1957).

SECOND INSTAR—The second instars spent an additional 3 to 7 days on the female's dorsum prior to dispersing. After dispersion each young scorpion was sorted into an individual container on 25 May 1977. Mortality due to starvation was very high: of the 70 individuals alive on 25 May, four died during May, 49 during June, and six during the first two weeks in July. Mortality was about equal among the three litters. The eleven surviving individuals entered the second molt at an age of 116 ± 20.7 days (mean \pm standard deviation) (range 81-158 days). Four of the second instars were unable to completely free themselves from their exuvium and died during the molting process.

THIRD INSTAR—There were no deaths during this stage. However, five of the seven specimens died from complications during, or shortly after, the molt to fourth instar. This stadium lasted 84.0 ± 46.5 days (range 36-143), and the molt to fourth instar occurred at an age of 200.6 ± 48.8 days (range 136-250).



Figs. 1-2.—Frontal view of female *Megacormus gertschi* Diaz giving birth in the laboratory: 1, note the randomly positioned young on her dorsum, and those in the birth basket which is formed by the first pair of legs only; 2, close-up showing the tail-first emergence of one young, and the anterior movement of the first instars on their ascent to the female's dorsum.

FOURTH INSTAR—The two specimens that entered this stage died of unknown causes 2 and 3½ months after the successful molt. The duration of this and subsequent stages are unknown.

Morphometrics, growth factors, and instar predictions (see Materials and Methods) on the life history of *M. gertschi* appear in Table 1. Measurements of seven specimens of various sizes, including three females from this study (known to be sexually mature), and published data (Soleglad 1976) from two adult females from other populations are also given in Table 1. A male and female from the same population on which this study is based correspond very well with the predicted dimensions for sixth and seventh instars respectively (Table 1). The values observed in adult females fall within the predicted 95% confidence interval for eighth instars in the case of metasomal segment V length and pedipalp chela length. The observed upper range for carapace length exceeds the predicted upper limit for eighth instars, but does not reach the predicted lower limit for ninth instars. Three of the five adult females, however, have carapace lengths that fall within the predicted range for eighth instars; and the two females that do not, correspond to eighth instars in the two other structures measured. Therefore, I consider that *M. gertschi* attains sexual maturity with the eighth instar.

Mating behavior.—Two matings were staged using the same male. The first female was mated on 27 November 1977, 205 days after giving birth. The proceedings were not observed, but a post-insemination spermatophore was recovered (Francke 1979). This female died seven days after mating.

The second female was mated on 26 February 1978, 297 days after giving birth. This mating took place 91 days after the male's previous mating. The following notes, with time of day at the left, summarize the observations on courtship and mating:

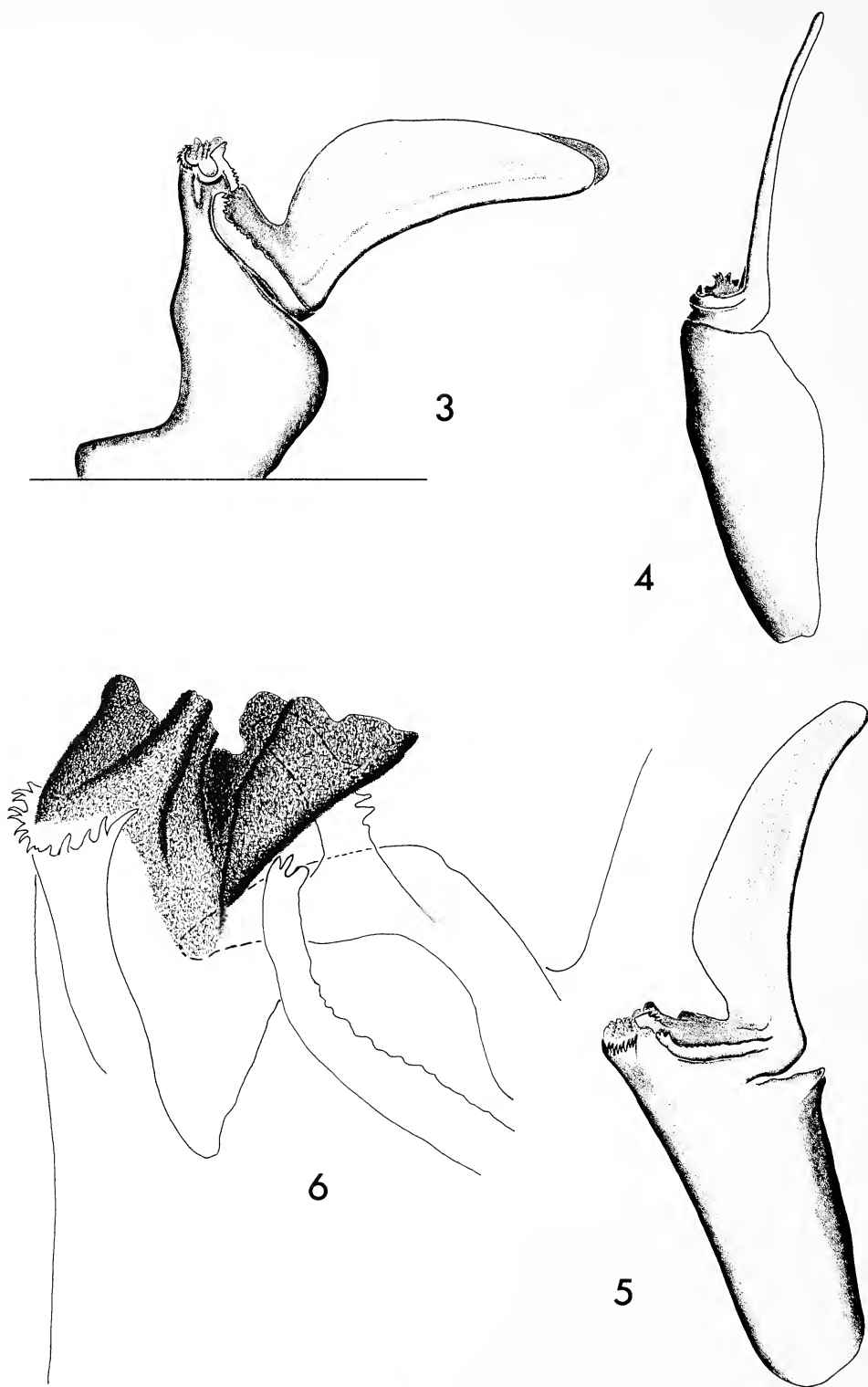
- 0930 - Male and female transferred from individual containers to mating arena.
- 0932 - Male approaches female from rear left, walks over female and moves away. No observable reaction by female.
- 0935 - Male approaches female frontally and grabs her pedipalps. Male's pedipalp chelae are outside female's chelae; the finger tips of female's chelae are slightly open and directed anteromedially. Male grips the manus of female's chelae.
- 0936 - Male stings female at anterior membrane of right tibia-chela joint. No reaction by female, her metasoma is curled to the left and resting on the substrate.
- 0944 - Male withdraws stinger (after nine minutes of continuous penetration), and a small drop of hemolymph appears at the puncture site on female. Male continues to grip female's pedipalp chela at arm's length. Male stings female at anterior membrane of left trochanter-femur joint. No reaction by female.
- 0945 - Male moves forward slowly, flexing his and her pedipalps. Chelicerae of male nearly touch chelicerae of female. Male moves back suddenly, extending pedipalps but maintaining grip, and thrusts strongly with stinger without previously withdrawing it.
- 0946 - Male moves forward again, although chelicerae do not touch, then moves back. While close to female, male extends the front pair of legs under her body, moving them slowly in an apparently exploratory behavior. The male's legs do not seem to reach female's genital opening. Male repeats the sequence of moving forward, extending the legs and moving back several times.
- 1003 - Male withdraws stinger (after nine minute penetration). No hemolymph seen at puncture site. Male moves forward, his chelicerae touch female's chelicerae, and then moves back. Female remains passive.

- 1004 - Male stings female at anterior membrane of left tibia-chela joint.
- 1007 - Male releases chelal grip on female's left chela; stinger remains inserted. Female does not withdraw left chela.
- 1008 - Male withdraws stinger (after four minute penetration). No hemolymph observed. Male moves forward, touching chelicerae with female's and moves back.
- 1009 - Male reestablishes chelal grip on female's left manus, and pulls female 5 cm forward (male moves backward). Male stings female at anterior membrane of right tibia-chela joint once again.
- 1014 - Male withdraws stinger (after five minute penetration). Male starts jerking backwards, pulling female forward, covering about 1 cm per jerk. Male's tail is extended back, parallel to substrate. After five jerks male stops and his genital opening touches the substrate.
- 1015 - Metasoma of male, still fully extended, is raised distally to form an angle of 30°-40° with substrate. Male's metasoma waves sideways slowly, spanning angles of 20°-30° to each side of the midline. Male raises the mesosoma straight up off the substrate and the spermatophore is extruded.
- 1016 - Male moves backward, pulling female forward. Female's genital opening is almost directly over the spermatophore. Male releases grip on female's pedipalp chela; reaches inside her partially extended pedipalps, and grabs her pedipalp femora. Male's pedipalps are flexed, pulling him closer to female; his chelicerae are over and above those of female. Female squats on the spermatophore. A "sparring" bout follows: both animals bring their tails forth and jab at each other with their stingers. Male releases grip on female's pedipalp femora, extends his pedipalps sideways, and vigorously claps at her sides with them. Female moves back about 1.5 cm, and extends her pedipalps in front. Female moves forward towards spermatophore, extends her chelicerae and grips the base of the spermatophore with her right chelicera.
- 1017 - I gently push female backwards with the blunt end of a pencil to save the spermatophore. Male remains undisturbed while female moves back about 2 cm and remains stationary.
- 1020 - Female turns about 160° to the left and moves away. Both specimens are returned to their individual containers.

Comparisons of the behavior patterns observed in *M. gertschi* with those reported for other scorpions is premature at this time because only one complete sequence was observed. For recent comparative analyses of courtship and mating behaviors in scorpions see Garnier and Stockmann (1972), and Polis and Farley (1979). They report that "sexual stinging" during courtship occurs in chactids (*Euscorpis* spp.), bothriurids (*Urophonius* spp.), and scorpionids (*Pandinus* sp.). Dr. Stanley C. Williams (pers. comm.) has also observed this behavior in several vaejovids. The evolutionary significance of this behavior is not clear.

Spermatophore description.—The following account is based on the study of two post-insemination spermatophores (from the same male) recovered during mating behavior studies, and one hemispermaphore (pre-insemination condition) dissected from a second male for comparative purposes. The terminology used is after Francke (1979).

Lamelliform (Figs. 3-5). Pedicel 1.20-1.30 mm long, 0.75-0.85 mm wide; pedal flexure conspicuous in post-insemination condition only (Fig. 3). Trunk 1.50-1.60 mm long,



Figs. 3-6.—Male reproductive structures of *Megacormus gertschi* Diaz: 3, lateral view of post-insemination spermatophore; 4, ventral view of hemispermatoaphore; 5, lateral view of hemispermatoaphore; 6, detail lateral view of capsular region of hemispermatoaphore.

Table 1.—Morphometrics, growth factors, and instar predictions on the life history of *Megacormus gertschi* Diaz. Measurements (in millimeters) represent the length of the structures indicated (mean \pm standard deviation). Data from Sogleglad (1976) indicated by an asterisk.

	Carapace	Metasoma V	Pedipalp chela
OBSERVED			
Second instar (n=7)	1.58 \pm 0.06	1.06 \pm 0.05	2.54 \pm 0.08
Growth factor	1.30 \pm 0.06	1.35 \pm 0.06	1.30 \pm 0.05
Third instar (n=7)	2.06 \pm 0.15	1.44 \pm 0.13	3.31 \pm 0.19
Growth factor	1.23 \pm 0.08	1.27 \pm 0.08	1.29 \pm 0.04
Fourth instar (n=5)	2.51 \pm 0.08	1.84 \pm 0.17	4.25 \pm 0.22
Average growth factor (n=12)	1.27 \pm 0.08	1.32 \pm 0.08	1.30 \pm 0.04
PREDICTED 95% CONFIDENCE LIMITS			
Fifth instar	2.91–3.47	1.81–3.05	4.73–6.32
Sixth instar	3.69–4.40	2.39–4.02	6.15–8.21
Seventh instar	4.69–5.59	3.15–5.31	8.00–10.68
Eighth instar	5.96–7.10	4.16–7.01	10.40–13.88
Ninth instar	7.56–9.02	5.49–9.75	13.52–18.04
FIELD CAUGHT SPECIMENS (RANGE)			
Adult females (n=3)	6.60–7.30	5.80–6.50	11.40–12.20
Adult females (n=2)*	6.65–7.30	5.80–6.40	11.65–12.75
Subadult female	5.60	5.00	9.20
Juvenile male	4.00	3.30	6.50

0.55–0.65 mm wide, depth could not be accurately determined. Truncal flexure marked by strongly sclerotized transverse lateral ridges that prolong ventrally into blunt edge of lamellae. “Capsule” strongly developed, everted in both the pre-insemination (Fig. 5) and post-insemination (Fig. 3) states. Capsular region roughly resembles a truncated tetrahedron: the plane area between the paired transverse ridges that mark the truncal flexure represent one face of the tetrahedron, and the planes between the transverse ridges and the dorsal seam of the spermatophore (where the two hemispermatophores come together) form the other two faces. The base (=fourth face) of the tetrahedron is imaginary and lies inside the trunk. The truncated “peak” of the tetrahedron is the opening of the sperm tube. Submedially along the dorsal seam are two heavily sclerotized bands that culminate each in a half-crown of sharp, curved spines (Figs. 3, 5, 6). The “V-shaped” areas between these submedian bands and the transverse lateral ridges (Figs. 5 and 6), are membranous and transparent, extend beyond the sclerotized portions of the capsular region, and distally their external surface is densely covered with minute, slightly to moderately curved spines (Fig. 6). Lamellae 2.00–2.30 mm long, 0.25–0.35 mm wide, 0.75–0.90 mm deep; thickened ventrally but not curled into an inverted “T-beam”, with dorsal margin slightly notched basally (Figs. 3, 5).

Among chactids only the spermatophores of *Euscorpius* spp. (Euscorpioninae) and *Superstitionia donensis* Stahnke (Superstitioninae) have been previously described (Angermann 1955, 1957, Angermann and Schaller 1956, Francke 1979). The spermatophores of *Megacormus gertschi* Diaz (Megacorminae) resemble those of *Euscorpius* spp. more closely than either of them resembles the spermatophores of *Superstitionia*. Based on the disposition of the ventral carinae on the metasoma, Birula (1917) suggested that

Euscorpioninae and Megacorminae are sister-groups within the Chactidae. More recently, Soleglad (1976) arrived at a similar conclusion based largely on a comparison of trichobothrial patterns between representatives of various chactid subfamilies. The spermatophore data available seem to lend further support to this phylogenetic interpretation. However, spermatophore information is needed for other subfamilies and genera before reasonable phylogenetic hypotheses can be developed.

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THE MORPHOLOGY AND THE RELATIONSHIPS OF THE LEPTONETIDAE (ARACHNIDA: ARANEAE)

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ABSTRACT

The tracheal apparatus of the Leptonetidae is examined; there are considerable differences between some genera. The taxonomic position of the family is discussed; they can not be related to any family of the "Haplogynae" by known shared derived characters.

INTRODUCTION

Until twenty years ago the Leptonetidae were a small group, known in life only to a few arachnologists. The recent discovery of more than a hundred new forms in the Mediterranean region, East Asia (Japan and Korea) and North America (USA and Mexico) has done little to change this.

Since most of the species are known only from caves, only the few cave specialists have had a good opportunity of examining material.

Much is still to be learned, especially of the biology and reproductive behavior of members of this family; also, the taxonomic position of the Leptonetidae is still unclear.

OBSERVATIONS ON THE RESPIRATORY APPARATUS

Some authors (e.g., Levi 1967:577) have thought the Leptonetidae lungless, although all species examined have indeed normal booklungs (personal observations; Fage 1913:490, Machado 1945:132).

A detailed study of the lungs has not been made. The number of leaves is low (Fage also saw only "quelques feuillets") and in general appearance these lungs are similar to those of some *Ochyrocera*, while in some Erigonidae, Linyphiidae and Theridiidae of similar size (*Diplocephalus*, *Centromerus*, *Porrhomma* and *Theonoe*) the lungs appear more developed. The tracheal apparatus however, which is quite conventional in position, is more interesting than the lungs.

Lamy (1902) found in *Leptoneta microphthalmia* Simon a very normal tracheal apparatus with a single slit-like spiracle which communicated with a wide vestibule; from

the vestibule originated four simple tracheal tubes. Machado (1945) found a similar condition in a Portuguese *Leptoneta*; and I in a Mexican *Neoleptoneta* (Fig. 4). Such an apparatus exists in many spiders. A curious Portuguese *Paraleptoneta* (named by Machado in 1951) had instead two clearly separated tracheal spiracles, not united by a vestibule (Machado 1945). Such an apparatus, with simple posterior trachea, is typical of the family Telemidae.

No Leptonetidae I examined had an apparatus of this kind, but three Mediterranean species [*Leptonetela strinatii* (Brignoli), *Sulcia cretica* Fage and *Barusia aesculapii* (Brignoli)—I follow the taxonomical changes proposed by Kratochvil 1978] had an intermediate, undescribed system. In these species there is a wide, normal vestibule, and at each corner there is a spiracle (Figs. 3, 5, 6). The openings of these spiracles are reinforced, and clearly visible with a phase-contrast microscope. It is impossible to say if a slit unites them, as in *Leptoneta* and *Neoleptoneta*; in these forms the slit is a mere fold of the integument and a real opening is not visible. In my opinion it is not especially relevant to ascertain the presence of a functional slit; the most important point is the presence of two reinforced openings which correspond to the two separate spiracles observed by Machado in *Paraleptoneta synthetica*. Machado considered this species primitive; the forms with a vestibule, advanced. The species I observed would then occupy an intermediate position.

The tracheal tubes of *Leptonetela* are characteristic; those of *Barusia aesculapii* and *Sulcia cretica* are somewhat different because of the presence of two large trunks; at the corner of the vestibule from each trunk depart a large number of tracheal tubes.

In the Leptonetidae the respiratory apparatus is thus usually, relatively normal. This is rather puzzling if we compare them with the Telemidae and Ochyroceratidae which also contain small, nonsclerotized and hygrophilous spiders. As in these two families, one might expect the absence of lungs in at least some leptonetids.

On the other hand the Leptonetidae are more similar, in general size and relative development of the legs, to the larger Ochyroceratidae (*Ochyrocera* and *Altheopus*) that have lungs, than to the smaller genera of this family (*Speocera*, *Theotima*, etc.) and to the Telemidae. Unfortunately, as Levi (1967:582) already noted, we know little of the physiology of respiration in spiders, and it is difficult to evaluate the relative efficiency of the lungs and of the trachea. The correlation between hazard of water loss and reduction of booklungs suggested by Levi (1967) is an interesting hypothesis but we need more information on this subject before we will be able to understand why groups which ecologically appear similar do not have the same kind of respiratory apparatus.

I am unable here to discuss the second hypothesis of Levi (1967), that "the trachea of the larger Dysderoidea may represent a phylogenetic character inherited from smaller ancestors."

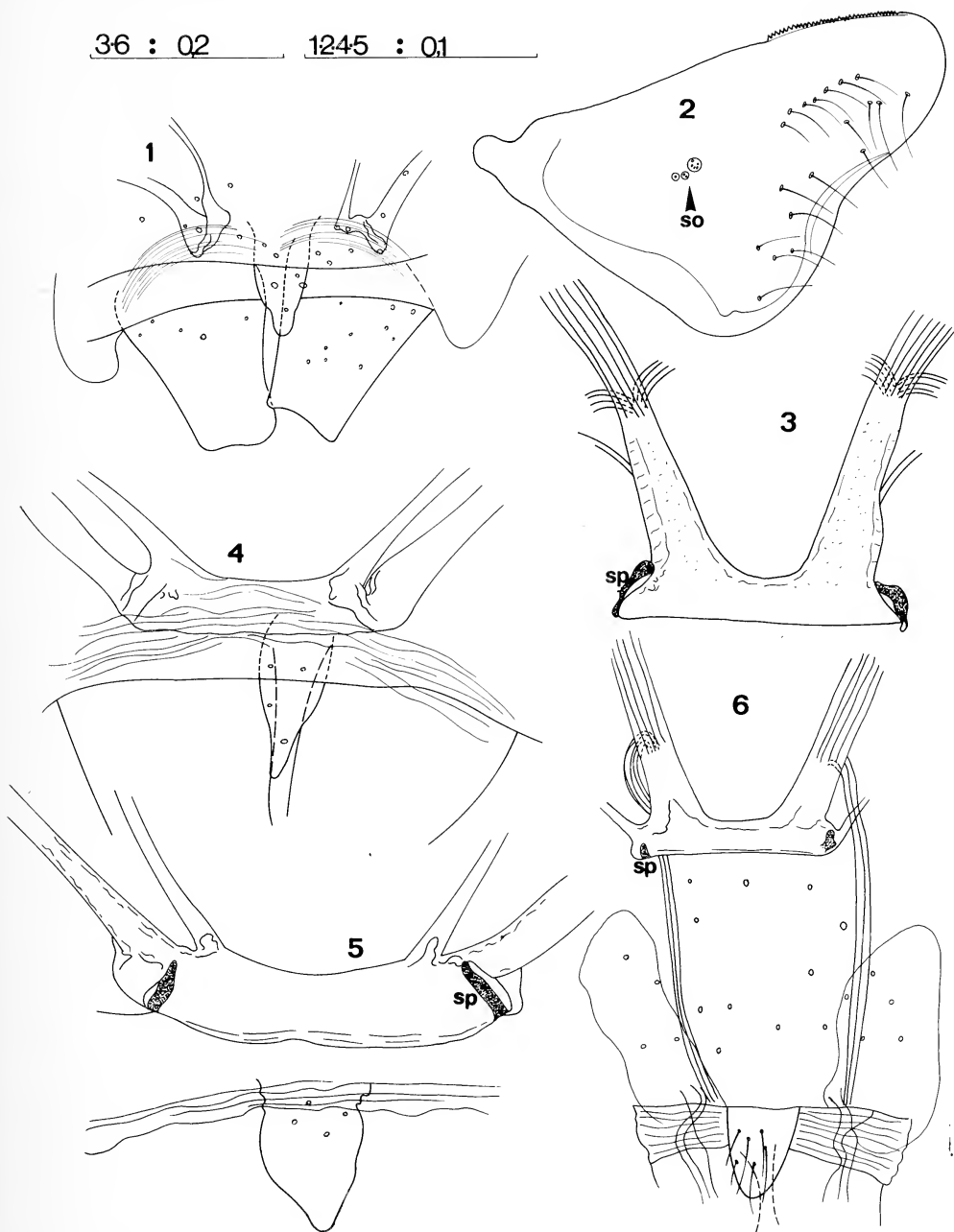
SOME OTHER MORPHOLOGICAL OBSERVATIONS

Male Genitalia.—The palpal bulb can be expanded, it is not immobile, as that of many Haplogynae. For illustrations of *Leptonetela* see Brignoli (1976). I have also recently observed the same fact in *Paraleptoneta spinimana*.

Female Genitalia.—The vulva consists always of two tube-like spermathecae, whose surface is covered by a glandular tissue and there are no fertilization ducts (the haplogyne condition according to Wiehle 1967); the atrium is relatively complicated and can pro-

36 : 02

1245 : 01



Figs. 1-6.—Morphology of the Leptonetidae: 1, *Neoleptoneta caliginosa* Brignoli, tracheal region (apparently there is no vestibule, but this is probably an artifact due to poor preservation of the abdomen); 2, *Leptonetela strinatii* (Brignoli), gnathocoxa showing "sensory organ" (=so); 3, *Sulcia cretica* Fage, tracheal region showing the wide vestibule and the two large lateral trunks; 4, *Neoleptoneta capilla* (Gertsch), tracheal region (note the similarity with *Leptonetela* and the absence of the sclerotized spiracle); 5, *Leptonetela strinatii*, tracheal region [identical is the same region of *Leptonetela kanellisi* (Deeleman-Reinhold)], spiracle = sp.; 6, *Barusia aesculapii* (Brignoli), tracheal region (note the considerable distance from the spinnerets). Scales in mm.

trude through the epigastric furrow. An expanded bulba (Brignoli 1975, Kratochvil 1978) resembles the condition found in some Linyphiidae. On the terminal part of the expanded vulva (which is like an inverted pouch) at each side of a hollow (but not always present) tongue-like structure is (always ?) a small porous plate similar to those found in some Scytodidae and most Pholcidae. The openings of the spermathecae, always difficult to see, are situated on the sides of the expanded (more or less triangular) vulva, near the porous plates (for illustrations see Brignoli 1979).

Gnathocoxae.—On the inner side of the gnathocoxae (Fig. 2) some structures are visible which are similar to the organ believed sensory also observed by Machado (1951) in the Ochyroceratidae. These structures could be identical with the “sexual glands” recently discovered in *Leptoneta microphthalmia* by Lopez and Emerit (1978). Since very few spiders have been examined carefully these structures may be present in most families.

THE TAXONOMIC POSITION OF THE LEPTONETIDAE

Most arachnologists have considered the Leptonetidae to belong to the haplogynes, which may be so if we consider the term “haplogyne” to have no phylogenetic meaning. They may be put in the Araneoidea (Archer 1948, Levi 1967) but no family of the Araneoidea seems related to them. Their expanded palpal bulb (Brignoli 1979) and their tarsal structures suggestive of a paracymbium recall some primitive Araneoidea such as the Tetragnathidae, but they do not seem to share any specialized characters with this family.

Until recently many authors have considered the Leptonetidae related to the Telemidae and Ochyroceratidae, perhaps because both these families are little known to most arachnologists and include small, rare and often cavernicolous species. Each of these three families is characterized by many autapomorphies:

Leptonetidae—six eyes in peculiar position (only exception *Archoleptoneta*); male palpal bulb little sclerotized, ending with many lamellae, expandable; expandable vulva with two spermathecae.

Telemidae—female genitalia with a single, large spermatheca (structurally different from those found in other haplogynes); with spermatophores [their existence, which I recently (Brignoli 1978b:113) suggested, has been demonstrated (Lopez, pers. comm.)]

Ochyroceratidae—chelicerae with median lamella (often with stridulatory grooves); vulva with two spermathecae, often curiously modified (for an explanation of this structure see Machado 1964); median spinnerets with a single spigot.

If we search for other characters we are hampered by our limited knowledge of haplogynes. The structure of the eyes, which has given many phylogenetic clues, has not been investigated in detail in the three families in question. According to Homann (1971) only the secondary eyes (*Nebenaugen*) are present in the families Dysderidae, Sicariidae and Oonopidae (and apparently also in other haplogynes). In the Leptonetidae and in the genus *Speocera* (Ochyroceratidae) the secondary eyes have no canoe-tapetum and are of a primitive type, as are those of the Orthognatha, Pholcidae, Urocteidae and Filistatidae. It can be concluded that the eyes of these families are not specialized.

The valuable paper by Kaestner (1953) on the structure and function of the chelicerae said little on most haplogynes; only some groups with a median lamella are discussed in detail (Filistatidae, Caponiidae, Scytodidae and Pholcidae). Kaestner noted many speciali-

zations (perhaps synapomorphies) in these groups, but the only explanation he could find (a secondary reduction due to the development of peculiar methods of capturing prey) is in my opinion only satisfactory for the Scytodidae.

From the scattered information we have on the development of the haplogynes we come to conclusions similar to those obtained from the eyes: the haplogynes and the Orthognatha (all ?) differ in their embryonic development from other spiders (Holm 1940). However, to share a primitive type of embryonic development is definitely not a synapomorphy.

There are no trichobothria on the tarsi of the Leptonetidae, Telemidae and Ochyroceratidae, but I am unable to estimate the phylogenetic value of this character, which has not been examined in many groups.

The palpi of the males of many Leptonetidae and Ochyroceratidae bear on their articles (femur, patella, tibia or tarsus) large, often transformed, spines or apophyses. Until their function is known it is questionable to consider them synapomorphic as many spiders of different families have similar structures.

Also until we know other haplogynes better, the large rhomboidal colulus and the four independent tracheal spiracles of the Telemidae have to be considered doubtful autapomorphies.

If we search for synapomorphies, we can find only that: (a) the chelicerae of the Leptonetidae and Telemidae are similar, but not specialized [those of the Ochyroceratidae are similar to those of the Scytodoidea (Brignoli 1975)]; (b) the position of the eyes of the Telemidae and Ochyroceratidae is the same as that of many six-eyed spiders; (c) the bulbs of the pedipalps of Telemidae and Ochyroceratidae are relatively simple, as are those of many haplogynes; and (d) the colulus of the Leptonetidae is similar to that of the Ochyroceratidae (and of most spiders). From these facts we can not conclude that these three families are closely related.

I referred the Ochyroceratidae to the superfamily Scytodoidea (Brignoli 1975), slightly different from the group proposed by Bristowe (1938). Recently (Brignoli 1978c) I am including the Filistatidae in the Scytodoidea. While the Dysderoidea seem to share important synapomorphies in the structure of the female genitalia (Brignoli 1975), the Scytodoidea are a much less natural group and may have to be divided.

The position of the Telemidae is still not clear, and much research will be necessary to ascertain if spermatophores are present in other families (I recall here the "strands" seen protruding from the palpal bulbs of some Oonopidae and Tetrablemmidae by Machado 1941, Brignoli 1974).

In 1975 I divided the haplogynes into four groups: one of these should be the Leptonetidae, for which a separate superfamily could be proposed. I still can not find any synapomorphies shared by the Leptonetidae and any other haplogyne family. The Dysderoidea have peculiar female genitalia (Brignoli 1975). The absence of the median lamella of the chelicera in the Leptonetidae (at present the only synapomorphy on which I base the Scytodoidea) excludes them from the Scytodoidea. A superficial examination of the genitalia might suggest relationships between the Leptonetidae and some Scytodoidea with two spermathecae (*Scytodes*, etc.), but in no family of the Scytodoidea has an expandable vulva been found. The specializations of the male tarsus of many Leptonetidae resemble those of some Ochyroceratidae and all Pholcidae, but this apparent synapomorphy is contradicted by the completely different structure of the female genitalia in these three families (personal observations on about 100 species in 25 genera of both Pholcidae and Ochyroceratidae).

The other families which I include provisionally in the Scytodoidea (Sicariidae, Diguettidae, Plecteuridae, Tetrablemmidae, Pacullidae and Caponiidae) do not share any derived character with the Leptonetidae.

Perhaps we will still find the relatives of the Leptonetidae. The curious genus *Physoglenes* Simon, 1904 (of which unfortunately no specimens survive) was thought to be a leptonetid by Simon, a theridiid by Fage, and a pholcid by Petrunkevitch (Brignoli 1978a). Future finds of this genus could be quite revealing.

To summarize, the Leptonetidae are not close to any other haplogynes and may belong in their own superfamily.

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***HUITACA VENTRALIS*, N. GEN., N. SP., WITH A DESCRIPTION OF A GLAND COMPLEX NEW TO CYPHOPHTHALMIDS (OPILIONES: CYPHOPHTHALMI)**

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ABSTRACT

Huitaca ventralis, new genus and species, is described from Colombia. Closest to *Metagovea*, the new genus differs in the form of the penis and ventral thoracic complex and proportions of the chelicera. A new exocrine gland complex, opening on the first abdominal sternite, is briefly described; its function is not known.

INTRODUCTION

The opilionid Suborder Cyphophthalmida is represented in South America by four genera. *Neogovea* Hinton includes two species from Guyana (Shear 1977), and two from Brazil (Hinton 1938, Martens 1969). *Metagovea* Rosas Costa includes two species, *disparunguis* Rosas Costa of Colombia (Rosas Costa 1950) and *oviformis* Martens from Brazil (Martens 1969). A species of *Metagovea* is also found in tropical Africa (Juberthie 1969). The remaining genus *Chileogovea* contains only the species *oedipus* Roewer; it is closely allied to genera from New Zealand and South Africa (Juberthie and Muñoz-Cuevas 1970).

The new genus described below is most closely related to *Metagovea*, but differs significantly in several particulars, especially in the form of the ventral thoracic complex and in having a type of exocrine gland not heretofore known from any opilionid.

At present no family designation is provided for *Huitaca ventralis* because of my conviction that the traditional placement of all cyphophthalmids in one family, with two rather arbitrarily characterized subfamilies, is unduly conservative. However, *Metagovea*, *Neogovea* and *Huitaca* would belong in Stylocellinae in the traditional scheme. In the context of a forthcoming review of the North American cyphophthalmid fauna, I will discuss the family classification and provide names for new family-level groups.

HUITACA new genus

Type Species.—*Huitaca ventralis*, new species, by present designation.

Diagnosis.—Distinct from *Neogovea* species in having a lamelliform (rather than brush-like) adenostyle, and from *Metagovea* species in the large eusternal sclerite present in males, as well as the dorsal (rather than ventral) opening of the adenostyle gland.

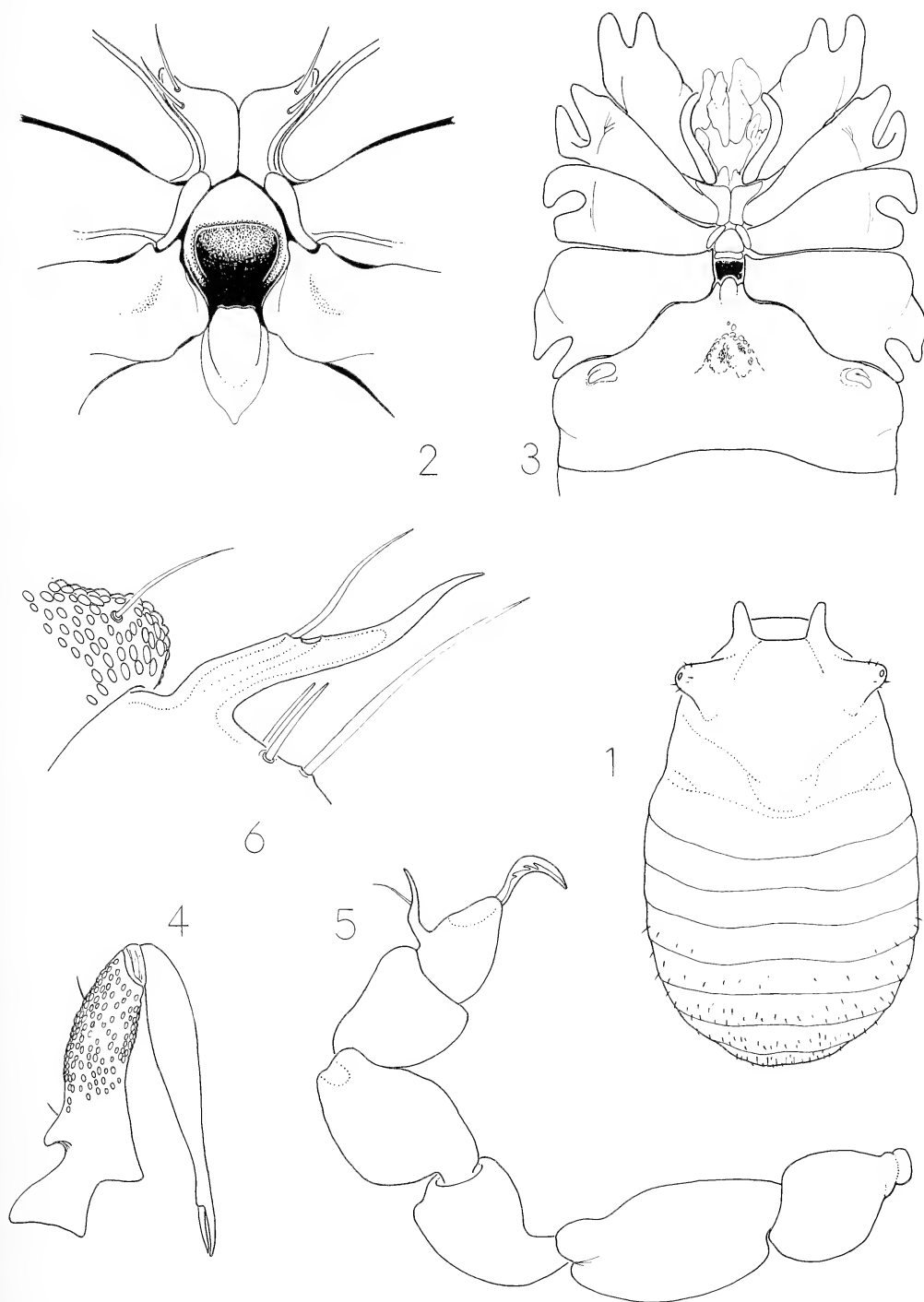
Description.—Medium sized cyphophthalmids of typical appearance. Grooves between abdominal tergites well-marked, median sulcus absent. Ozophores removed from cephalothorax margin, but not fully dorsal (Juberthie's Type II); opening terminal. Eyes absent. Anterior margin of scute with squared emargination above chelicerae, laterally prolonged as squared flange on each side of chelicerai insertions. Claws toothed. Chelicerai teeth uniform, blunt, few in number. Chelicerae with distal article about seven times as long as broad. Mesosterna present and of typical form; metasterna longer than broad, oblique, widely separated in the male by a large eusternum. Dorsal and anterior walls of gonostome formed by eusternum, lateral walls by reduced gonostomal lobes of fourth coxae, posterior wall by extension of abdominal sternite set off in a manner suggestive of nascent operculum. Abdominal sternite I with a unique exocrine gland, opening through paired complexes of pores. Dorsum lightly pebbled, with few setae; legs heavily pebbled. Fourth tarsus of male not divided; adenostyle long, acuminate-lamellate, pore dorsal. Male fourth metatarsi completely ornamented. Anal glands not detected. Penis with 10-12 setae in each lateral group, ventral plate with 17 or 18 short, thick apical setae; gonopore with membranous, fimbriate lateral lobes.

Etymology.—Huitaca was the moon goddess of the Chibcha people, who ruled north eastern Colombia before the Spanish conquest (Osborne 1968).

Remarks.—In comparison with the closely related *Metagovea*, similarities are the form of adenostyle (at the base of the tarsus, acuminate) and in the corona analis, a complete ring formed by the fusion of abdominal sternites eight and nine and tergite nine. The latter character is also found in *Neogovea*. *Huitaca ventralis* resembles *Neogovea* species in the form of the chelicerae, which have a slender distal article and a small movable finger; in *Metagovea* the distal article is only about four times as long as broad and the movable finger is one-fourth the length of the distal article. In all three genera, the chelicerai teeth are uniform and large; in *Neogovea* and *Huitaca* they appear as blunt nodules.

Neogovea kamakusa Shear has a small eusternal sclerite which, however, does not separate the metasterna. In *Huitaca ventralis*, this sclerite is larger than in any other cyphophthalmid and widely separates the metasterna, so that the gonostomal lobes of the fourth coxae do not meet anterior to the gonostome, as they do in both *Neogovea* and *Metagovea* species. Thus the eusternum forms more of the outer margins of the gonostome than observed in any other species of the suborder. In addition, the anterior projection to the gonostome of the first abdominal sternite is more lobe-like and clearly set off than in other cyphophthalmids, suggesting that the boundary between having a genital operculum and lacking one might not be as distinct as heretofore imagined (a genital operculum as a separate sclerite is found in Opiliones in the Laniatores and a few Troguloidea; in the majority of Palpatores the gonostome is partly or wholly covered by an unarticulated lobe of the first abdominal sternite).

As in *Metagovea*, the claws of *Huitaca ventralis* are toothed. One species of *Neogovea*, *N. mexasca* Shear, does not have teeth on the claws of legs I and II in the females, but this species is troglotic and may be aberrant.



Figs. 1-6.—Anatomy of *Huitaca ventralis* male: 1, body, dorsal view; 2, ventral thoracic complex, ventral view, (first coxae omitted); 3, anterior part of body, ventral view; 4, right chelicera, lateral view; 5, right leg IV, mesal view; 6, adenostyle, mesal view.

While conforming in general to the pattern found in related South American genera, the penis of *Huitaca ventralis* differs in the larger numbers of setae and the bizarre, unique fimbriate lobes surrounding the gonopore.

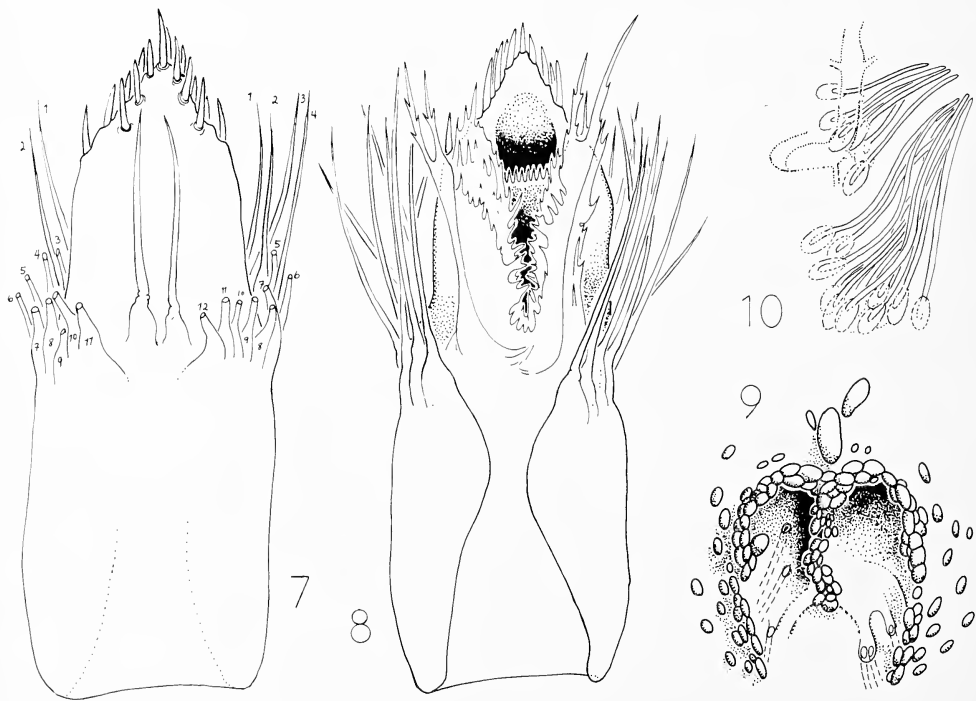
Martens (1969) described a cyphophthalmid from Brazil which he declined to place in a genus. Known only from a female, this species ("*enigmaticus*") has certain features suggestive of *Huitaca*, but the ventral thoracic complex is not clearly illustrated, nor is it described. In any case, the small size of Martens' specimen (1.45 mm long) precludes its conspecificity with *H. ventralis*.

Huitaca ventralis, new species

Figs. 1-10

Types.—Male holotype, one male and one juvenile paratype from 30 km south of Chinacota, elevation 320 M (8000'), Prov. Norte de Santander, Colombia, collected 14 May 1975 by Stewart B. Peck, deposited in Museum of Comparative Zoology, Cambridge, Mass., USA.

Description.—Taken from male holotype. Total length, 3.03 mm, width across ozophores 1.50 mm, greatest width (third abdominal segment), 1.58 mm. Dorsum (Fig.



Figs. 7-10.—Anatomy of *Huitaca ventralis* male: 7, penis, ventral view. Some setae of lateral groups shown as if cut, for clarity; 8, penis, dorsal view; 9, ventral view of openings of ventral abdominal exocrine gland complex; 10, dorsal (internal) view of ventral abdominal exocrine gland complex.

1) granulate, with scattered setae more densely set on posterior part of abdomen. Ventral thoracic complex as in Fig. 2; mesosterna typical, aracuate, anterior portions widest, broadly flaring. Metasterna oblong, oblique, completely separated by subtriangular eusternal sclerite extending antieriad from anterior lip of gonostome. Gonostomal lobes of fourth coxae very short, forming only posterior half of lateral lips of gonostome, anteriorly showing articulation with metasterna. Posterior lip of gonostome formed by well-marked lobular extension from first abdominal sternite. First abdominal sternite (Fig. 3) with openings of exocrine gland complex (see below). Spiracles kidney-shaped. Corona analis formed by complete fusion of sternites eight and nine and tergite nine. Anal region not modified.

Chelicerae (Fig. 4) typical; basal article 1.68 mm long, 0.45 mm wide; distal article 1.44 mm long, 0.23 mm wide; movable finger 0.29 mm long. Fingers with two or three noduliform teeth. Palpal trochanter scantily set near distal end with small pointed tubercles. Legs densely covered with pebbled cuticular pattern, pebbling absent from tarsus of fourth leg (Fig. 5). Adenostyle (Fig. 6) at tarsal base, sinous, lamellar-acuminate, as long as tarsus width, pore on dorsal side near midpoint, subtended by single seta. Measurements of legs and palpus as follows:

	palpus	I	II	III	IV
trochanter	0.39	0.38	0.36	0.30	0.38
femur	0.53	1.05	0.87	0.65	0.90
patella	0.35	0.60	0.47	0.56	0.63
tibia	0.44	0.80	0.60	0.59	0.68
metatarsus	----	0.47	0.57	0.41	0.53
tarsus	0.41	0.57	0.60	0.33	0.38

Penis in ventral view as in Fig. 7. Lateral groups of 10-12 setae each, ventral group of two; ventral plate with marginal setae short, stout, in two ranks, totalling 17. In dorsal view (Fig. 8) with large, flared, fimbriate structures around gonopore.

Color dark brown, appearing black without magnification.

Female unknown.

Distribution.—Known only from the type locality. The type locality is in the Cordillera Oriental, near the headwaters of the Rio Zulua, which flows north to Lake Maracaibo.

Etymology.—The specific epithet is an adjective referring to the exocrine gland complex on the abdominal venter.

Notes.—The ventral gland complex is further delineated in Figs. 9 and 10. Internally (Fig. 10) the complex appears to consist of two groups of small, multicellular gland units on each side. The anterior group of each side contains about six units, while the posterior group contains 12-15 units. Each gland unit has an independent duct, though not all the ducts could be traced to openings through the heavy cuticle of the sternite. In external aspect, the gland units are seen to open in a raised region of the sternite (Fig. 3, 9), delimited by cuticular tubercles formed by sequential enlargement from the normal sculpture of the body surface; the surface of the raised area is divided by a row of tubercles into two depressed regions. A few pores, with canals from gland units, were detected in these depressions.

Because the type collection consisted only of males, it cannot be assumed that this unique gland complex is a secondary sexual character. Likewise we have no clues to its functional significance, but Juberthie (1967) has described a gland complex dorsal to the

anus in *Siro rubens* which he speculated may have sexual significance, as it occurs only in males. Males of several South African and New Zealand genera have strongly modified anal regions, with brushes of setae which suggest a mechanism for the dispersal of a volatile pheromone. Juberthie and Muñoz-Cuevas (1970) describe a set of four rough knobs on the posterior part of the ventral surface of *Chileogovea oedipus*. They do not appear to be glandular. The glands I observed in *Huitaca ventralis* are similar in some features of their gross morphology to the anal glands described by Juberthie (1967); inappropriate preservation and scarcity of material precluded any histological studies. Behavioral studies would be useful in the clarification of the function of the anal glands of *Siro* and others, the abdominal-sternal glands of *Huitaca ventralis*, and indeed even the well-known glands opening through the adenostyle.

More closely related to *H. ventralis* is *Ogovea nasuta* Hansen, of the west African island of Fernando Póo (Hansen 1921). Through the courtesy of Dr. Henrik Enghoff of the Zoologisk Museum, K benhavn, I have been able to examine the type specimen of *O. nasuta* in detail. The males of this species have a strong, posteriorly directed projection extending from the first abdominal sternite, just behind the gonostome. Posterior to this projection is a deeply depressed oval area extending back to the anterior margin of the fifth sternite. A pair of grouped gland units occurs on each side near the base of the projection; pores from these glands appear to open on the margins of the projection itself. While Hansen (1921) described and illustrated the sternal modifications, he did not detect the associated glandular apparatus.

Juberthie (pers. comm. 1978) has in press a description of two species of cyphophthalmid from New Caledonia in which exocrine glands open through single mid-line pores on the third and fourth abdominal sternites. These glands seem quite different from those in *H. ventralis* and *O. nasuta*, and according to Juberthie, his species are more closely related to the "sironines" than the "stylocellines."

ACKNOWLEDGEMENTS

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PREY CAPTURE BY THE SCORPION *HADRURUS ARIZONENSIS* EWING (SCORPIONES: VAEJOVIDAE)

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ABSTRACT

Prey capture behavior of the desert scorpion *Hadrurus arizonensis* Ewing has been studied in the laboratory. Information about the behavior was obtained from analysis of ten 8mm movie films, and 50 direct observations of individual prey capture sequences. An ethogram was constructed which depicts the interrelationships between the discrete behavioral components; e.g., alert stance, grasp success, and sting. Most individuals also exhibit a pedipalpal sand thrust, which may function in a cleaning capacity.

INTRODUCTION

Scorpions are best known for their dramatic stinging behavior, which can be associated either with prey capture or with defense. Still, scorpion prey capture behavior has not been studied to any appreciable extent. Many previously published descriptions have been anecdotal in nature (Lankester 1883, Pocock 1893, Fabre 1911, Smith 1927). Several more recent articles do include brief descriptions of prey capture for various scorpion species (Vachon 1953, Baerg 1961, Cloudsley-Thompson 1961, Williams 1963, Stahnke 1966). Hadley and Williams (1968) maintained several species in the laboratory, and described the prey capture behavior of *Paruroctonus mesaensis* Stahnke as representative. Palka and Babu (1967) described the ballistic defensive movements of the scorpion *Heterometrus* spp.

Robinson and co-workers have studied the prey capture behavior of several tropical web-building spiders (Robinson 1969, Robinson and Mirick 1971, Robinson and Olazarri 1971, Robinson *et al.* 1971, Robinson and Robinson 1973, 1974). Ethograms of the predatory sequence were designed and intraspecific variations noted. Prey capture by a primitive web-builder (Valerio 1974) and by jumping spiders (Forster 1977) have also been studied.

This paper represents the results of a study similar to the above on the predatory behavior of a species of desert scorpion, *Hadrurus arizonensis* Ewing. The prey capture sequence is depicted in an ethogram, and the behavioral components are described.

METHODS

Individuals of *H. arizonensis* were collected in August 1977 near Palo Verde, California. The scorpions were maintained individually in 25 cm x 35 cm terraria, with 15 cm deep sandy-soil substrate, which permitted them to burrow. The individuals were of unknown age, ranging in length from 5 to 10 cm (prosoma to aculeus), and weighing from 0.89 to 7.36 grams. In the holding room, fluorescent lights and two heat lamps were on fourteen hours and off ten hours, daily. Temperatures ranged respectively between 20° and 29° C. Water was provided weekly by misting the substrate and by saturating a sponge, upon which the scorpions were seen to knead with their chelicerae, presumably extracting the moisture. Individuals were removed from their terraria for observation only after onset of the dark period, when they were out of their burrows. The observation and filming chamber was semicircular, with a 50 cm diameter.

Nymphs and adults of the American cockroach, *Periplaneta americana*, and adults of the common house cricket, *Acheta domesticus*, were offered to the scorpions as prey. Orthoperan species have been identified as natural prey for *H. arizonensis* (Hadley and Williams 1968). Time between feedings varied from one week to one month.

Ten prey capture sequences were filmed with a Beaulieu 4008 Zm 11 Super 8mm movie camera, at 24 frames per second and analyzed with a Kodak stop action projector. No overt differences were noted between the behavior when filmed under white lights and that observed under red light. The spectral sensitivities of *H. arizonensis* photoreceptors have not been described, so it is not known whether or not the red light can be perceived.

The next stage of the study involved 50 prey capture sequences by fourteen individuals, viewed under two 40W red tungsten light bulbs. Each scorpion was transferred with forceps to the observation chamber and after a thirty-minute acclimation period, the cockroach or cricket was introduced. Subsequent activities were recorded on a cassette tape recorder for later transcription.

RESULTS AND DISCUSSION

The prey capture sequence, as observed and analyzed in the laboratory, is represented by the composite ethogram (Fig. 1). The terms used in the ethogram are defined as follows:

Motile—locomotion within the chamber, prior to contact with the prey.

Retracted—body in contact with the substrate, metasoma and appendages drawn in.

Alert Stance—a posture in which the scorpion is supported above the substrate by the legs, the pedipalps are extended anteriorly, with the movable fingers of the pedipalpal chelae and the pectines in contact with the substrate (Fig. 2).

Orientation—movement of the scorpion resulting in the anterior aspect being directed towards the prey.

Grasp Attempt—an effort to obtain a hold on the prey with the pedipalpal chelae.

Grasp Failure—the prey escapes after a grasp attempt, whether there is contact or not.

Grasp Success—the scorpion obtains a firm hold on the prey with at least one pedipalp.

Sting—a behavioral unit consisting of a forward sweep to the metasoma, telson contact with the prey and subsequent probing movements, and aculeus penetration with presumed venom injection.

Inactive—following a grasp success; no visually detectable activity of chelicerae, pedipalps or walking appendages.

Manipulation—handling of the prey by the pedipalps and first pair of legs, including turning of the prey for head-first ingestion.

Cheliceral Activity—protraction of one chelicera and retraction of the second, alternating with retraction of the first and protraction of the second. The chelicerae are opened during protraction and closed during retraction.

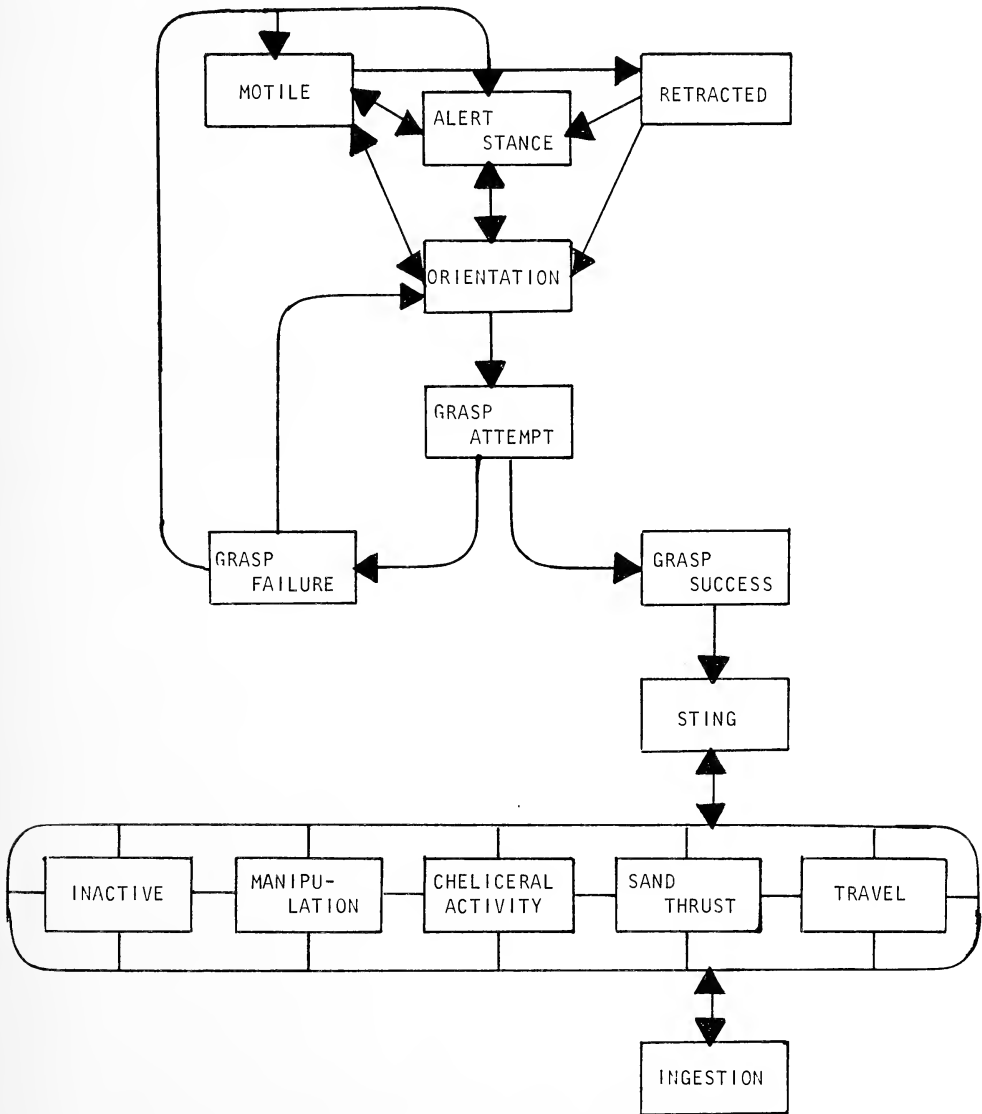


Fig. 1.—Ethogram of the prey capture sequence and its constituent behavioral units for the scorpion *Hadrurus arizonensis*. Individual terms are defined in the text. Behavior observed in this study was seen to flow in the direction of the arrows. The box circumscribing five of the behavioral units indicates that any of these units can precede or follow any of the others.

Sand Thrust—a pedipalp is pushed into the substrate, withdrawn, and frequently brushed off by the distal segments of the first and second pair of legs.

Travel—moving throughout the chamber, holding the prey in a pedipalp and/or chelicerae.

Ingestion—the intake of the pre-digested fluid prey, as indicated by cyclical movements of the coxae of the first legs.

The Prey Capture Sequence.—Many individuals, when first placed in the observation chamber, moved around the area in an exploratory fashion before settling. A potential prey encountered during this motile stage, either was ignored by the scorpion, or induced orientation and a grasp attempt. When a scorpion ceased to move around the chamber, it usually adopted one of two postures. In some sequences (20%), the scorpions took on a retracted posture with the ventral surface resting on the substrate, and the pedipalps, legs and metasoma drawn in against the body. In a few cases, scorpions in a retracted posture completely ignored prey. At other times, however, the scorpion responded to nearby prey by taking an alert stance or by making an immediate grasp attempt.

In most instances (80%), the scorpion adopted an alert stance (Fig. 2) soon after being placed in the observation chamber. In this posture, the prosoma and mesosoma are supported slightly above the substrate by the four pairs of legs and the metasoma is curled dorsomedially. The pedipalps are extended anteriorly, slightly bowed. The chelae are open, with the very tips of the movable fingers in contact with the substrate. The distal aspects of the pectines are also touching the ground. Occasionally, scorpions would lift their pedipalps and pectines, reorient by moving forward or pivoting, then re-adopt the alert stance. This activity often results in directed orientation of the scorpion towards nearby prey.

A scorpion in the alert stance was able to detect and orient to moving prey and to make a grasp attempt before there was direct contact. Immobile prey did not elicit either orientation or grasp attempts. On several occasions, a scorpion and prey would both stand perfectly still within a few centimeters of each other for several minutes. Should the prey move first, the scorpion would lunge and often successfully grasp it, but when the scorpion moved first, the prey would usually avoid capture. The use of substrate-borne vibrations for prey detection by *H. arizonensis* seems quite possible. Brownell (1977) demonstrated the ability of another vaejovid desert scorpion, *Paruroctonus mesaensis*, to detect compressional and surface waves generated by digging activity of prey up to a distance of 50 cm. Electrophysiological recordings showed that compound slit-sensilla on the basitarsal leg segments, and tarsal hairs responded to these prey-generated, substrate vibrations. Analogous sensory mechanisms may be operating in *H. arizonensis*, possibly with auxillary input from mechanoreceptors on the pedipalps and pectines, which are both in contact with the substrate during the alert stance.

The alert stance of *H. arizonensis* brings legs, pedipalps, and pectines in contact with the substrate simultaneously. The stereotyped placement of these appendages in this behavior may be critical in permitting central nervous system integration of environmental information concerning prey location. Another arthropod, the water strider *Gerris remiges*, utilizes a comparable stereotyped posture during prey orientating behavior (Murphy 1971). Localization of a stimulus and subsequent responses by this organism are determined by which of the six legs are closest to the stimulus.

Even though the mechanical senses may be of highest importance, the prospect that the visual system plays a role in prey location should not be discounted without direct experimentation. Recent studies (Fleissner 1977a,b), demonstrate the high sensitivity of scorpion photoreceptors, particularly the lateral eyes.



Fig. 2.—The alert stance of *Hadrurus arizonensis*, in which the distal aspect of the pectines and the tips of the movable fingers of the pedipalpal chelae are in contact with the substrate.

Fig. 3.—*Hadrurus arizonensis* stinging an adult cockroach on the ventral surface. Note the involvement of both the mesosoma and metasoma in telson placement, and the supportive positioning of the legs.

In grasp success, both pedipalps are employed, with one or both gaining a firm hold of the prey. In 61% of the sequences, the first grasp attempt was successful, while in the other 39%, two or more attempts were necessary. The attempt was considered a grasp failure if the prey was missed altogether, or was held only momentarily before escaping. Under natural conditions, should the scorpion fail in a grasp attempt, it is most likely that the prey, unless injured, would move from the vicinity and thereby reduce the prospects for a second attempt. In this study, where escape was not possible, the scorpions were allowed unlimited grasp attempts.

The prey was stung at least once in all sequences observed. When stinging prey, *H. arizonensis* maintains postural stability by extending the second, third and fourth pairs of legs in a characteristic pattern (Fig. 3). The first pair of legs may be supportive as well, but more frequently assists the pedipalps in the manipulation of the prey. The thrashing legs of the victim may be held or moved aside by these anterior most legs. The pectines remain inactive during stinging, being withdrawn against the ventral mesosomal surface. The telson is initially brought forward dorsomedially in a slow precise movement (Fig. 4). The posture of the mesosoma during stinging ranges from a slight convex bowing

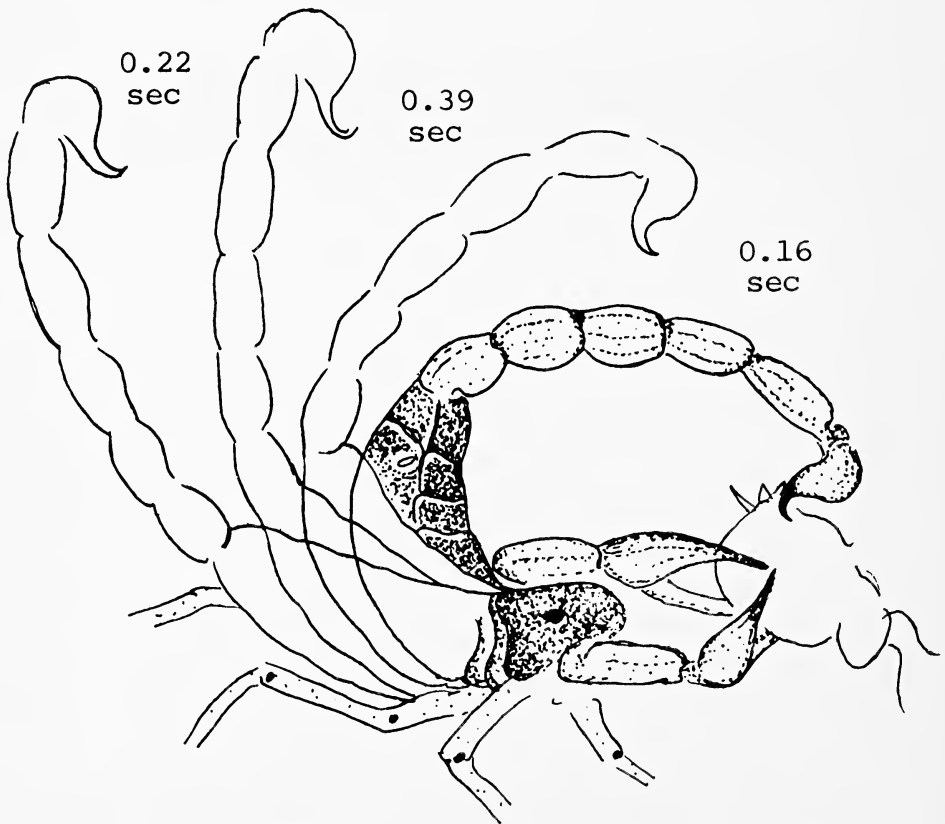


Fig. 4.—Progressive movements of the opisthosoma from point of grasp success to telson contact. Tracings are from selected frames of an 8mm movie taken at 24 fps. Time periods between positions are given, the entire movement taking approximately 0.75 seconds.

involving every segment (Fig. 5A), to a more angular deflection (Fig. 5B). It is the metasoma, however, which demonstrates the greatest flexibility. As opposed to the more or less uniplanar curving of the mesosoma, the first four joints of the metasoma have a considerable rotational ability (Bowerman 1972). When the telson is brought forward, the aculeus first contacts that part of the prey's body in direct line with the sweep. If soft tissue of the prey is met, penetration and presumably venom injection occur immediately. However, if hard chitinous plates are contacted first, the telson must then be repositioned to locate a penetrable tissue.

Some species of scorpion (e.g., *Euscorpius italicus* and *Anuroctonus phaidactylus*) seldom, if ever, employ a sting during prey capture (Schultz 1927, Cloudsley-Thompson 1955a, Baerg 1961, Williams 1963, McDaniel 1968). Baerg (1961) points out that scorpions with large pedipalps and reduced metasoma probably do not use the sting for immobilizing prey. In the current study, *H. arizonensis* stung every prey offered. It is possible that *H. arizonensis* may not sting prey below a certain size, or under different conditions, but these were not investigated.

The time from telson contact to actual penetration by the aculeus, i.e., that time spent locating soft tissue, ranged approximately from one to 50 seconds. In some cases, extensive telson movements occurred throughout this period.

Steiner's (1976) mapping of predatory digger wasp sting sites on cricket prey showed clumped distribution, positively correlated with the location of major ganglia. There appears to be no such correlation in the sting sites of *H. arizonensis* on either cricket or cockroach prey. Rather, the sting site distribution appears to reflect the sites of the first penetrable tissue encountered. Adult cockroaches, for example, received 94% of the

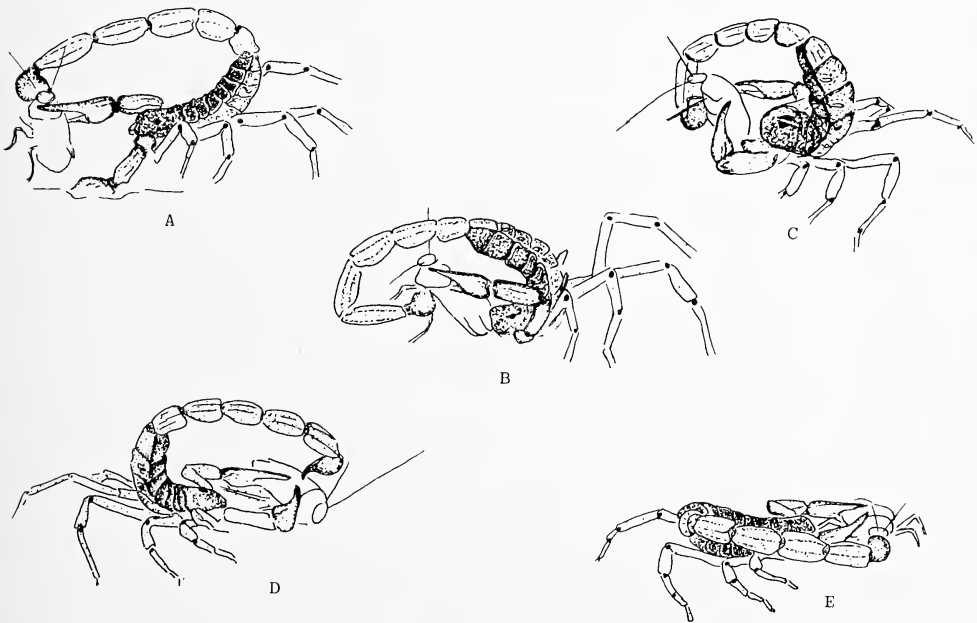


Fig. 5.—Postures demonstrated by *Hadrurus arizonensis* when stinging prey. Drawings are from single frames of 8mm movies.

stings on their ventral surface, even though the dorsal surface was usually encountered first by the telson. The heavy wings and thoracic sclerites appear to prevent dorsal penetration. Adult cricket prey, however, received 75% of their stings dorsally. The dorsal aspect was again usually encountered first, but since the relatively small cricket wings do not extend over the abdomen, immediate penetration could often occur.

Any one of the behavioral units following the sting, may follow any other as shown by the box and interconnections in the ethogram (Fig. 1). For example, the initial sting may be followed by inactivity, manipulation, cheliceral activity, sand thrusts or travel. Subsequent stings occurred in 52% of the sequences, usually in response to struggling of the prey.

Within this part of the prey capture sequence an interesting behavior termed the sand thrust occurs which heretofore has not been described. The sand thrust (Fig. 6) was observed in 81% of the sequences and appears to be a fundamental part of prey capture in this species. Only one individual repeatedly failed to exhibit the sand thrust. Four other scorpions failed to exhibit the sand thrust in one of several observed sequences. The remaining nine scorpions invariably performed the sand thrust during the prey capture sequence.

Either simultaneously with, or following a sting, the scorpion releases one pedipalpal chela from the prey while retaining hold with the other. The free pedipalp is thrust into the sandy substrate up to the base of the chela. Usually, it is withdrawn immediately, but at other times it is kept buried for several seconds. Repetitive thrusts frequently occur, and prior to regrasping the prey, the chela is often brushed off by the distal segments of the ipsilateral first and second legs. A sand thrust by one pedipalp is sometimes immedi-



Fig. 6.—The sand thrust behavior demonstrated by *Hadrurus arizonensis* following the capture of prey.

ately followed by a sand thrust with the other pedipalp. The function of the sand thrust behavior is unknown. It may well be a grooming or cleaning behavior, as hemolymph from the prey often contacts the pedipalps during capture.

In the majority of the sequences (75%), the scorpions remained to feed at the site where the prey was captured. In the other sequences, they traveled throughout the observation chamber with the prey held in one pedipalp or the chelicerae. This activity continued occasionally interspersed with digging behavior, until the scorpion eventually settled to feed.

Chelicerel mastication began at the head end of the prey in 89% (39/44) of the sequences. In 30 of the sequences, this required that the prey be reoriented by manipulation with the pedipalps. In each of the other nine sequences, the prey was caught in such a way that the head was already directed toward the chelicerae. Other manipulations involved displacement or removal of the prey's wings, leg and/or antennae. The head first prey consumption seen in *H. arizonensis* has been described in *Opisthophthalmus latimanus* Koch by Alexander (1972), who identified the position of the prey's legs as being one of the clues used by the scorpion for feeding orientation. The possible advantages underlying this specific head-first ingestion were not discussed in her article. Head-first consumption may assist in subduing the prey by immediately damaging the brain. Alternatively, the scorpion may be avoiding the posterior aspect of the prey, since many orthopterans have large powerful legs which could greatly interfere with the feeding activities of the scorpion. Similarly, chemical defenses in some prey such as tenebrionid beetles are extruded from the rear, and would be avoided by starting at the head.

The scorpion's first pair of walking legs aid the pedipalps in manipulating prey, which is not an unusual characteristic among the arachnids. Within the Solifugae and Amblypygi, the first pair of walking legs are secondarily segmented for use as tactile organs, and are not used for locomotion (Savory 1970). Certain Araneae are known to use their first pair of legs for display during courtship, as well as for walking. Bowerman (1975) in a study on the control of walking in *H. arizonensis*, noted that the first pair of legs exhibited different stepping patterns than the more posterior legs, i.e., they were elevated for longer periods during stepping. It was suggested that these legs functioned, in part, in a tactile capacity. A closer investigation of these appendages in several scorpion species would be of interest.

The chelicerae are activated prior to their actual contact with, and use in, mastication of the prey. The activity consists of reciprocating movements of left and right appendages. One chelicera is protracted with open chela, at the same time that the other chelicera is retracted with closed chela. Then, each chelicera performs the motion just completed by the other. The reciprocate grasping and retraction by the two chelicerae slowly tears the prey's exoskeleton, exposing the inner tissues to the digestive enzymes of the scorpion (Snodgrass 1948). Rhythmic movements of the coxae of the first pair of legs help in transporting the predigested prey into the scorpion's oral cavity by means of a pumping action (Shrivastava 1955). Observations on the prey capture sequences were terminated when the rhythmic movements of the coxae signaled that ingestion had commenced.

Predation strategies of several species of desert scorpions have been observed in the field. In general, the majority of these scorpions employ a sit and wait strategy (Williams 1963, Stahnke 1966, Hadley and Williams 1968, Enders 1975), ambushing prey that blunders into the vicinity (Pianka 1973). Some large diplocentrid species wait in the entrance of their burrows, while most of the vaejovid species move a distance from the

burrow before settling. *H. arizonensis* appears to utilize a sit and wait strategy involving the alert stance. The presumption that the prey capture sequence of *H. arizonensis* unfolds similarly in the field to the way it does in the laboratory observation chamber awaits verification. However, given that the just stated presumption is reasonably sound, the current study provides an informational foundation for further studies on the feeding behavior of *H. arizonensis* as well as for comparative studies of other species of scorpion, both closely and distantly related.

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CUPIENNIUS SALEI KEYS. (ARANEAE)
IN THE HIGHLANDS OF CENTRAL GUATEMALA

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ABSTRACT

Cupiennius salei Keys. was collected in the highlands of central Guatemala near Cobán (departamento Alta Verapaz). It was found mostly on agaves and on banana plants in coffee plantations near the tropical rain forest. The favorite retreat is at the base of agaves and behind the trough-shaped basal parts of banana leaf sheaths. Showing pronounced rhythmicity in its diurnal locomotor activity, the spider leaves its retreat after dusk to hunt; cockroaches and earwigs were the animals most frequently preyed upon. Included is an account of recent research on this species and of the geographic range and taxonomic placements assigned to it in the literature.

INTRODUCTION

Cupiennius salei Keys. has attained great significance in many aspects of spider research. We know many details about its reproductive and prey catching behavior (Melchers 1963, 1964, 1967), the fine structure of its cuticle (Barth 1969, 1970, 1973), the biochemistry of its hemocyanin and muscle metabolism (Loewe, Linzen and Stackelberg 1970, Loewe and Linzen 1975, Linzen, Angersback, Loewe, Markl and Schmid 1977, Linzen and Gallowitz 1975), the fine structure of its hemocytes and Malpighian tubules (Seitz 1975, 1976), and its embryology and development (Melchers 1963, Seitz 1966, 1967, 1970, 1971). In our own work we have used *Cupiennius* to study strain detection in the exoskeleton by the slit sensilla and the role these organs play in behavior (Barth 1967, 1976, 1978, Barth and Bohnenberger 1978, Bohnenberger 1978, Seyfarth 1978a, b). It has been shown electrophysiologically in this species that the Blumenthal tarsal organ is an odor chemoreceptor (Dumpeert 1978).

All these studies were done with offspring bred in the laboratory from animals found in banana shipments of unknown origin (Melchers 1963). There have been no reliable descriptions of the habitat in which *C. salei* lives nor of its behavior in the field except a few, general remarks like those of Vellard (1936).

The growing importance of this species as a laboratory animal warranted a new effort to locate and observe *C. salei* in its natural environment. After reviewing the literature Central America seemed to be the most promising area for a search. In March 1977 we collected *C. salei* in Guatemala. The present paper deals with our field observations and reviews previous reports in the literature on its range and various taxonomic assignments.

OBSERVATIONS

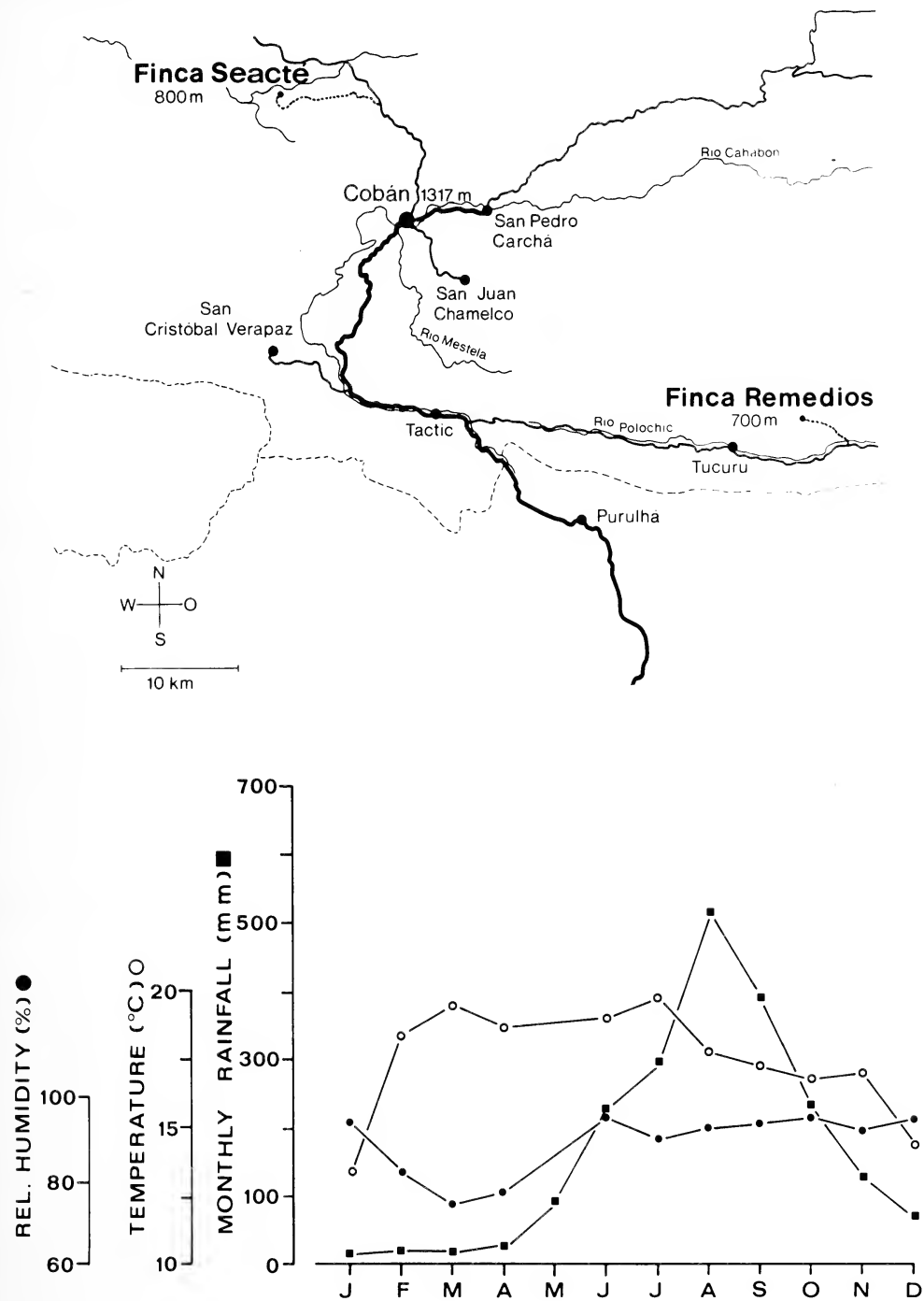
Habitat.—The two areas (Finca Seacté and Finca Remedios) where we found *C. salei* are located in the highlands of central Guatemala in plantations close to Cobán, the capital of the departamento Alta Verapaz (Fig. 1). The elevation of these two places near the neotropical rain forest is 700 and 800 m, respectively. The climate is that of the *tierra templada*: average temperatures range from about 15°C to 20°C with highest readings around May; rainfall is heaviest between August and October, and the dry season lasts from November to about May; the relative humidity is about 90% year round (Fig. 2).

On these plantations banana plants (*Musa sapientum* var. *prusna*) are cultivated as protective shade trees for young coffee plants. Typically *C. salei* lives on these banana plants (Fig. 3). More rarely we found it on agaves (*Furcraea melanodonta* and *Sansevieria* sp.). A few individuals were caught in the immediate vicinity of a finca house in crevices under a tin roof and among a pile of tiles. Young spiders were also found among decaying banana leaves on the ground. Although we searched extensively both during the day and at night we did not find a single individual within the rain forest proper.

Neither banana nor coffee plants, however, are sufficient guides to *C. salei*. We did not find it in the large banana plantations of the warmer lowlands (*tierra caliente*) of the Southwest between Escuintla and San José (departamento Escuintla) nor in the hot and humid area around Flores in the northern lowlands of the Petén. We also searched unsuccessfully in coffee plantations (with banana plants) close to the Lago de Atitlán (departamento Sololá) and on the southern slope of the Volcán de Agua (departamento Escuintla). Likewise, we were unable to find any specimen in Puerto Rico in the Cordillera Central near Maricao or in the Luquillo Mountain Range. Both of these regions belong to the same climatic zone as Alta Verapaz in Guatemala.

A common feature of the plants inhabited by *Cupiennius salei* is the fleshy, mechanically strong character of their leaves and, above all, the trough-like shape of their basal parts, which provide shelters for the spiders. Here they sit prosoma down during the daytime and much of the night (see below) without building any kind of a web. This also applies to females carrying an egg sac. We never found any sort of spider-built retreat. On banana plants the almost closed space formed by the sheaths of outer leaves of the pseudostem is the preferred hiding place (Fig. 3). Here the spiders are protected from direct exposure to sunshine as they are at the base of agaves. Even as late as 11 a.m., when the air temperature had risen to 30°C, spiders in these retreats had their hairy bodies still covered with dew. Some individuals always returned to the same retreat for up to one week, which was the longest period of time we were able to observe at any one location. Others had left their original plants after only one night.

Figure 4 shows the number and distribution of individuals found in the coffee plantation of Finca Remedios close to Tukurú (Fig. 1). We counted 50 individuals in a sample area of 2,750 m² with a total of 131 banana plants. With one exception the 14 individuals found in the leaf litter on the ground were young spiders with a leg span of 6 cm or less, i.e. younger than the eighth moulting stage (Melchers 1963). As a rule the



Figs. 1-2.—Habitat of *Cupiennius salei* Keys. in Guatemala, Central America: 1, location of Finca Seacté and Finca Remedios in the departamento Alta Verapaz; 2, climate of habitat shown by monthly averages of temperature, relative atmospheric humidity, and rainfall. Humidity and temperature values were measured for Finca Seacté in 1975/76, whereas the rainfall data were taken at Finca Remedios and are means for the period from 1972 to 1976.



Fig. 3.—Habitat of *Cupiennius salei* Keys.: Finca Remedios, Alta Verapaz; pseudostems of banana plants within coffee plantation with typical retreats behind leaf sheaths (arrows).

larger stages sat on the pseudostem of the banana plant not more than 1 m above the ground. This corresponds to the observed locations of the retreats behind leaves. Generally we found just one subadult animal at any one time on small agaves and small banana plants, but up to three or four spiders on large plants, usually with one adult among them.

The animals closely match the pattern and coloration given by Melchers (1963), with the exception that adult females tend to be somewhat darker. Since May 1977 we have successfully bred spiders caught in Guatemala with specimens of our original laboratory-raised stock.

Diurnal Rhythmicity.—*Cupiennius salei* has a pronounced diurnal locomotor rhythm (Seyfarth, in prep.). During daytime it is not seen outside its retreat, except occasionally in the very early morning hours. It hunts at night. The onset of locomotor activity is very abrupt. After sunset, at light intensities of about 20 Lux (measured with a calibrated light meter), *C. salei* turns around so that its prosoma points upwards. It remains motionless in this position above its retreat for about half an hour until it is completely dark to the human eye (illumination level below 0.1 Lux). Then the spider starts moving slowly up a leaf to wait for prey. This sequence of events is typical and stereotyped and was seen in many individuals. The time of return to the retreat varies, some spiders being back after three or four hours, others much later. In no case did *C. salei* return immediately after a catch. Instead they fed on their prey wherever they had caught it.

Prey.—The onset of hunting activity in *C. salei* after dusk coincides with the first appearance of a number of potential prey insects like cockroaches, earwigs, flies, crickets,

grasshoppers, and moths. *Cupiennius salei* was seen with specimens of all these insects between its chelicerae, but cockroaches were the prevalent prey in the area studied at that time of the year (March). They were identified as *Epilampra maya* Rehn and *Panchloria* sp., most likely *alcolhua* S.&Z. (Blaberidae), as *Ischnoptera rufa* DeGeer and *Ischnoptera* sp., close to *tolteca* Saussure (Blattellidae). The earwigs preyed upon were *Doru taeniatum* Dohrn (Forficulidae).

The pronounced restriction of hunting activity to the dark period underlines the importance of mechanical signals for prey identification and localization by *C. salei*. Prey is not actively pursued. In general the spider waits motionless until its victim comes within range of a quick and precise jump. It is well known that both air movements and

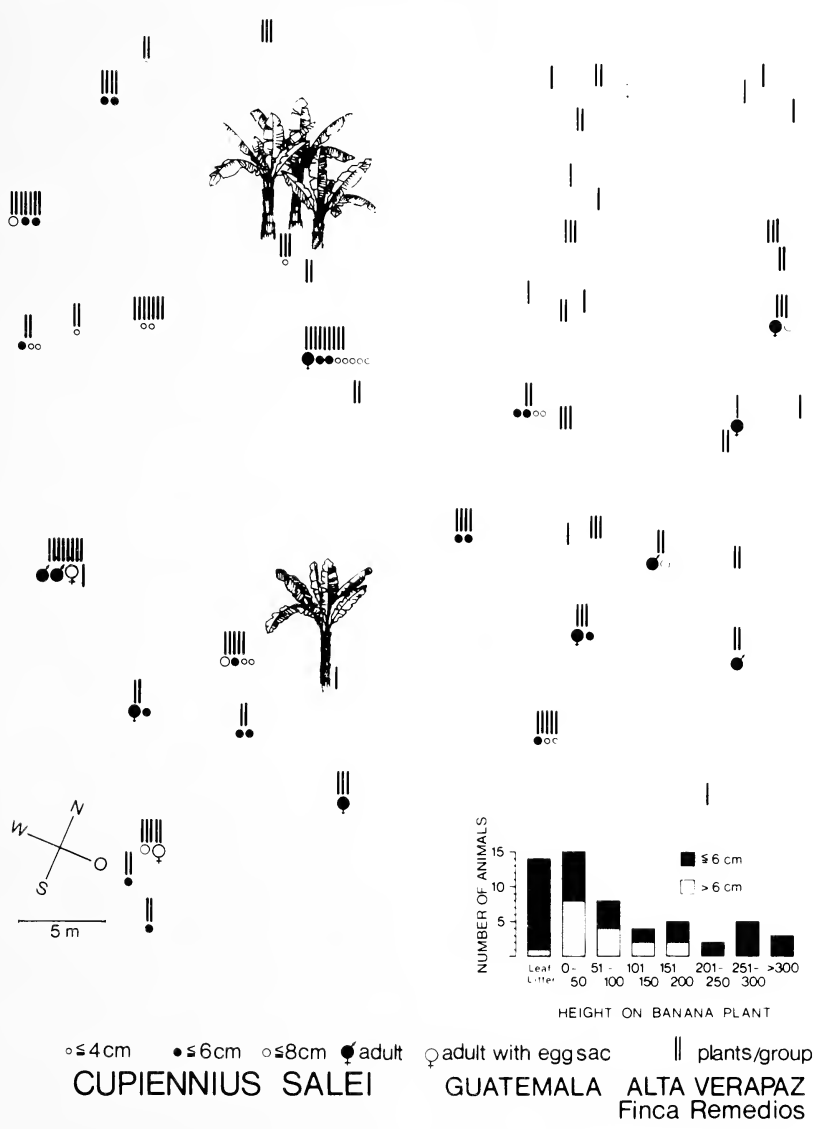


Fig. 4.—Number and distribution of *Cupiennius salei* Keys. in a sample area (Finca Remedios) 2,750 m². Vertical bars symbolize banana plants standing either singly or in groups. Vertical distribution of animals is shown by graph on lower right.

Table 1.—Summary of reports on *Cupiennius salei* Keys., including synonymies, taxonomic assignments, and geographic range. Only such sources listed which state or imply that specimens were newly collected. Therefore accounts such as Comstock (1912), Mello-Leitão (1936), Bonnet (1945), and Levi et al. (1968) not included here. An asterisk (*) indicates family assignment used for the first time.

BINOMIAL	FAMILY	ORIGIN	AUTHOR
1. <i>Ctenus saléi</i> n.sp.	* Ctenoidae	South America Mexico (Veracruz)	Keyserling (1877)
2. <i>Phoneutria oculifer</i> n.sp.	* Ctenidae	Mexico	Karsch (1879)
3. <i>Cupiennius oculatus</i> n.sp.	* Clubionidae	Guatemala	Simon (1891, 1897)
4. <i>Ctenus mordicus</i> n.sp.	Ctenidae	Guatemala (Salinas de Nueve Cerros)	O. P.-Cambridge (1892)
5. <i>Ctenus saléi</i> Keys. <i>Cupiennius oculatus</i> Simon	"Cteniform"	Guatemala, South America, Mexico	F.O.P.-Cambridge (1897)
6. <i>Cupiennius salei</i> Keys.	* Pisauridae	Mexico, Guatemala, Honduras, Costa Rica, Panama	F.O.P.-Cambridge (1901)
7. <i>Cupiennius salei</i> Keys.	Ctenidae	Florida (Lake Worth)	Banks (1904)
8. <i>Cupiennius salei</i> Keys.	Pisauridae	Costa Rica (Surubres, 250 m)	Banks (1909)
9. <i>Cupiennius salléi</i> Keys. = <i>Phoneutria oculifera</i> Karsch	Pisauridae	Brasil (Pará) Rio Hondo (?)	Strand (1910)
10. <i>Cupiennius salei</i> Keys.	Ctenidae	Panama	Petrunkévitch (1925)
11. <i>Cupiennius salei</i> Keys.	Pisauridae	Mexico (Veracruz)	Roewer (1933)
12. <i>Cupiennius salei</i> Keys.	Ctenidae	Panama (Barro Colorado Island)	Chickering (1936)
13. <i>Cupiennius salléi</i> Keys.	Pisauridae	Guatemala	Schmidt (1954)
14. <i>Cupiennius salei</i> Keys.	* Lycosidae	Laboratory-bred	Homann (1971)

substrate-carried vibrations caused by potential prey are the signals decisive for prey detection. Measurements with a capacitive transducer probe show that vibration signals caused by prey and carried across an agave leaf remain strong enough to be detected by a *Cupiennius* sitting at least 20 cm away from the vibration source. Comparable results are expected with the banana pseudostem. The frequency power spectrum contained in such natural vibrations is characterized by low frequencies with a maximum below 30 Hz (Barth, in prep.).

DISCUSSION

Apparently the chief climatic requirements of *C. salei* are moderate daytime temperatures (approximately 25°C) and a high degree of humidity (see also Melchers 1963a). Both conditions prevail in the observed, typical retreats behind leaves of banana stems or at the base of agaves. Concurrently these plants are a substrate for prey catching. *Cupiennius salei* hunts at night, thus again behaviorally avoiding the heat extremes. Actograph measurements as well show that it restricts its locomotor activity to the dark period of the day (Seyfarth, in prep.). We therefore assume that normally also searching for sexual partners, mating, and moulting take place during the night. Although we did not find *C. salei* in the tropical rain forest adjoining the plantations, we do not exclude the possibility that the species inhabits suitable forest plants like epiphytic bromeliads. Obviously *C. salei* did not evolve in plantations and in fact Chickering (1936) reports it as occurring in the forests of Barro Colorado Island, Panama.

Table 1 summarizes previous reports on the origins and range of *C. salei*. The findings in Mexico, Guatemala, Costa Rica, and Panama are comparatively well documented, but characterizations of the various habitats are lacking in all cases. The report of a *Cupiennius* found in Florida (Banks, 1904) is apparently based on a single specimen; most of the *Cupiennius* in the Harvard collection were found in fruit stores of the eastern USA, i.e. were introduced to the USA in fruit shipments from abroad. We conclude that *C. salei* lives throughout Central America, possibly including some Caribbean islands, but is unlikely to occur in the continental USA or South America (pers. comm. with local arachnologists).

There is also no general agreement on the systematic position of *C. salei*. In order to stimulate taxonomic work with this widely used laboratory spider, we have also included in Table 1 the variety of names and taxonomic assignments given to the species. Although we presently do not contribute new data to the controversy of the systematic position of *Cupiennius* we particularly want to draw attention to the work of Homann (1961, 1966, 1971, 1975), who has included *C. salei* in his comparative studies. According to Homann the Lycosidae, Pisauridae, and Ctenidae cannot be separated from each other as families. In a way this statement mirrors the fact that in the previous literature all three families are offered for *Cupiennius*. Homann considers them subfamilies (Lycosinae, Pisaurinae, Cteninae) of the Lycosidae. Among several arguments he stresses similarities of eye anatomy and ontogeny. All the above "lycosids" have three pairs of secondary eyes with a grate-shaped tapetum and rhabdoms arranged in rows.

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RESEARCH NOTES

ADDITIONAL RECORD OF *HETERONEBO* FROM ABD-EL-KURI ISLAND, P.D.R. YEMEN (SCORPIONES: DIPLOCENTRIDAE)

The genus *Heteronebo* Pocock was originally established for two species, *Heteronebo granti* Pocock and *Heteronebo forbesii* Pocock, from the island of Abd-el-Kuri, P.D.R. Yemen (Francke, O. F. 1977. J. Arachnol. 4:95-113). I indicated then that I had some reservations about the accuracy of the locality data accompanying the five known specimens of *Heteronebo*. Those reservations were largely based on the similarities between *Heteronebo* spp. and some undescribed diplocentrids from the Caribbean region. Subsequently, I revised the diplocentrid scorpions from circum-Caribbean lands, recognized six additional species of *Heteronebo* from the Greater Antilles, and included *H. granti* and *H. forbesii* among the Antillean fauna on the grounds that accurate locality data were unavailable for them and they might eventually be collected in that region (Francke, O. F. 1978. Spec. Pub. Mus. Texas Tech Univ., Lubbock, No. 14, 92pp.).

Dr. Jürgen Gruber (Naturhistorisches Museum Wien, Austria) recently sent me two additional immature specimens of *H. forbesii* from Abd-el-Kuri [Insel Abdal-Kuri, C. Simony leg., 1899..XXII]. Since the individuals and dates involved in the collection of the two available samples of *Heteronebo* from Abd-el-Kuri are different, I no longer have any reason to question the accuracy of the locality data or the presence of *Heteronebo* there.

I have been unable to find any significant generic differences between *Heteronebo* spp. from Abd-el-Kuri and those from the Greater Antilles. The age of the seven known specimens from Abd-el-Kuri, however, is not known, and it is possible that sexually mature individuals (confirmed by examination of the reproductive systems) might exhibit differences that would warrant the creation of a new genus for the Caribbean taxa.

The two new specimens of *H. forbesii* can be briefly characterized as follows:

(1) immature female: carapace length 3.65 mm, pedipalp chela length 5.10 mm. Pectinal tooth count 8-8. Pedipalp femur longer than metasoma segment IV. Tarsomere II spine formula 5/5 5/5 : 5/5 5/5 : 6/6 6/6 : 6/6 6/6.

(2) immature male: carapace length 3.05 mm, pedipalp chela length 4.40 mm. Pectinal tooth count 10-10. Pedipalp femur longer than metasoma segment IV. Tarsomere II spine formula 5/5 4/4 : 5/6 5/5 : 6/6 6/6 : 4/4 6/6. Carapace abnormal, lacking anterior median notch (anterior margin entire). The two specimens conform with other *H. forbesii* in most respects (Francke 1977, 1978, *op. cit.*), differing from the lectotype in having the pedipalp femur longer than metasoma segment IV. This character, therefore, is no longer useful in separating this species from *H. granti* (see Francke 1977, *op. cit.*, p. 109).

I am thankful to Dr. Gruber for allowing me to examine the specimens, and to Mr. David Sissom for his comments on the manuscript.

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DESIGNATION OF A LECTOTYPE FOR *PHRUROTIMPUS* *MINUTUS* (ARANEAE: CLUBIONIDAE)

A problem often faced by practising taxonomists is the loss or deterioration of type-specimens, which are the name bearers of species. A holotype or syntypes definitely known to have been destroyed may be replaced by a neotype, provided the rather stringent conditions laid down by the International Code of Zoological Nomenclature are met. If the type-specimens are partly or wholly in existence, the taxonomist's task is generally easier, though the condition of the specimens may be critical. In this paper we examine a nomenclatural problem in the clubionid genus *Phrurotimpus*, and take a first step toward its solution by designating a specimen from the original type-series as lectotype.

The spider species *Phrurotimpus minutus* (Banks, 1892) was described, in the combination *Phrurolithus minutus*, from an unstated number of specimens collected along two gorges that empty into Cayuga Lake in northern New York State (Banks, N. 1892. Proc. Acad. Nat. Sci. Philadelphia, pp. 11-81). Banks' description pertains solely to the adult female, though he included illustrations of both the epigynum and the adult male palpus. Because no reference was made to types, we can assume that the primary type-series consisted of at least one female and one male. Emerton (J. H. 1911. Trans. Connecticut Acad. Arts Sci. 16: 385-407) later collected and redescribed an adult male from Tyngsboro, Mass., and Kaston (B. J. 1948. Bull. Connecticut St. Geol. Nat. Hist. Surv. 70: 1-874) followed with new illustrations of Emerton's male and of an adult female from Woods Hole, Mass.

Phrurotimpus minutus is to be included in our forthcoming manual of sac spiders, which treats all of the species known or assumed to occur in Canada and Alaska. However, Banks' original figure of the epigynum is not sufficiently diagnostic to permit positive identification of the species. The female figured by Kaston (*loc. cit.*, fig. 1349), in our opinion, represents *P. dulcineus* Gertsch, 1941, a species of which the adult male is known and which differs specifically from the male that Banks identified as *P. minutus*. Examination of the type-series was essential; this was facilitated through the kindness of Dr. H. W. Levi, Museum of Comparative Zoology, Harvard University (MCZ).

The type vial of *P. minutus* contains the following: one adult female without appendages, one adult male with both palpi intact but without legs, one juvenile specimen without appendages, and the excised tarsus of an adult male palpus. The epigynum of the female is in poor condition, having the parts warped and darkened so as to obscure the outlines of the copulatory openings and spermathecae. Immersion in clove oil did not improve it. It is, in our opinion, unreasonable to attempt to diagnose *P. minutus* on the basis of this female, even though Banks heavily emphasized it in his original description. The two males in the type vial, on the other hand, are in full agreement with those illustrated by Banks, Emerton, and Kaston.

Few additional specimens of *P. minutus* have been collected. The MCZ has Emerton's male from Tyngsboro, MA. The American Museum of Natural History (Dr. N. I. Platnick, Curator) has three adult males collected respectively at Chicago, IL, Ithaca, NY, and Lakehurst, NJ. Other specimens labelled as *P. minutus* in these collections are misidentified representatives of other species.

We believe that stability of nomenclature is best served if Banks' figured (though not verbally described) male with intact palpi is regarded as part of an original syntype series

and designated as lectotype of *P. minutus*. This would permit diagnosis of the species in a way consistent with the diagnoses made by all subsequent authors who have dealt with it. The adult female of the species must, however, remain undiagnosed until specimens undisputably associated with adult males become available.

We therefore designate the syntype male as illustrated in Figure 67b of Banks (*loc. cit.*) as lectotype of *P. minutus*. This male is deposited in the MCZ and bears the following labels: *Phrurolithus minutus* Banks, 1892, Ithaca, NY, Nathan Banks Collection, LECTOTYPE MALE designated by Dondale and Redner 1979; Museum of Comparative Zoology. The original syntype female, the juvenile specimen, and the excised male palpal tarsus in the type vial are labelled PARALECTOTYPES (other data as for lectotype).

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A NEW *PARAPHRYNUS* FROM YUCATAN (AMBLYPYGIDA, TARANTULIDAE)

A new eyeless cave species belonging to *Paraphrynus* has been sorted out from a collection of amblypygids made in Yucatan. This is the first species described in the genus in which all eight eyes are absent. This lack of eyes as well as unusual pedipalp spination make it quite distinctive from all other known species of *Paraphrynus*. The following description is based on the female holotype.

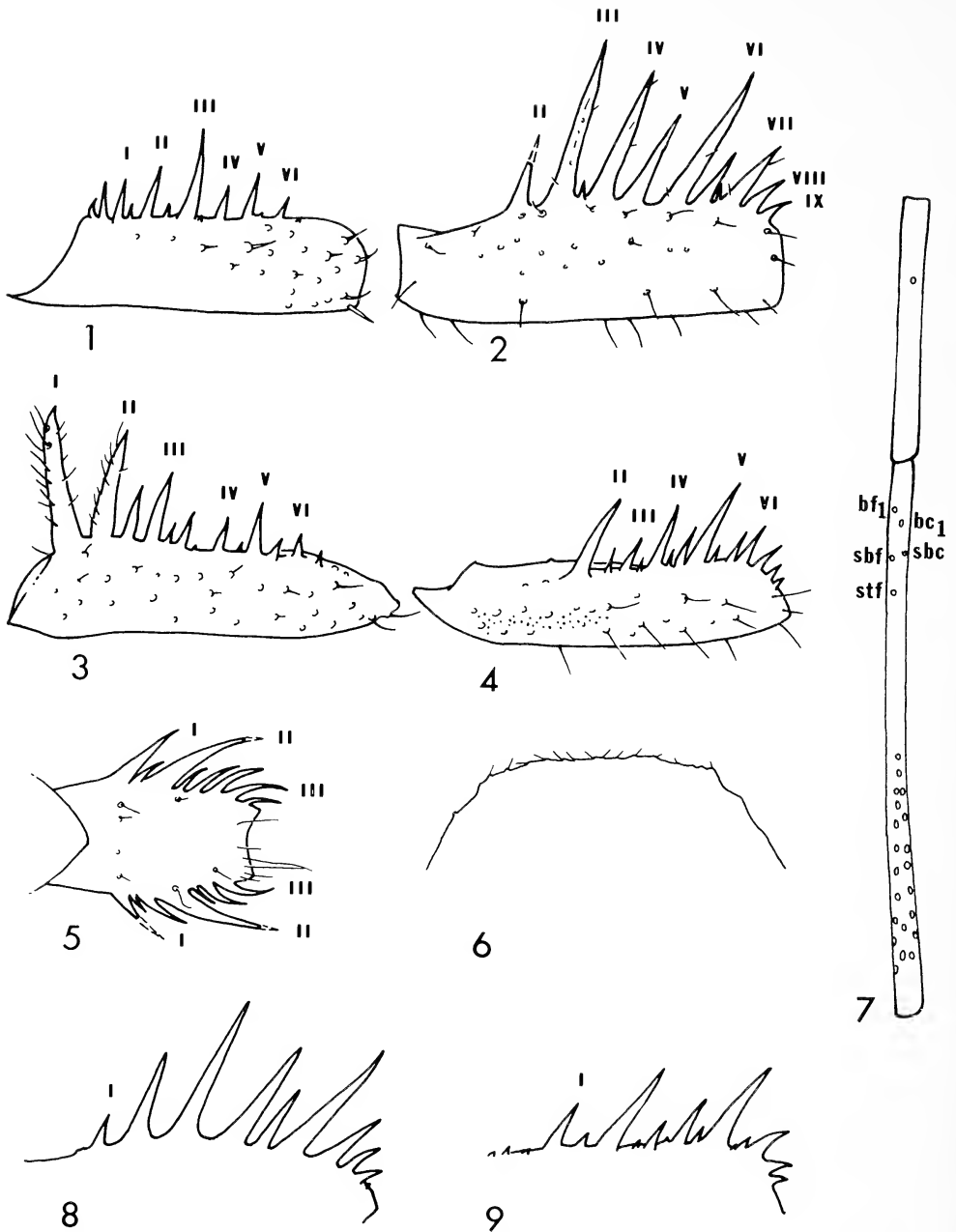
Paraphrynus reddelli, new species

Figs. 1-9

Types.—Female holotype and female paratype from Actún Loltún, 7 km SSW Oxkutzcab, Yucatan, Mexico (25-26 July 1975. James Reddell, Andrew Grubbs, David McKenzie, Suzanne Wiley). Both deposited in The American Museum of Natural History.

Diagnosis:—General color a pale brown with no conspicuous banding. Carapace lacking eyes. Can also be distinguished from other described species of *Paraphrynus* by pedipalp spination. On ventral surface of pedipalp femur there is a well developed spine between spines II and III (fig. 3). This spine is lacking in all other species of *Paraphrynus*. On pedipalp tibia the spines corresponding to I on dorsal and ventral surfaces are lacking (figs. 2, 4). This spine occurs on both surfaces in all other species of *Paraphrynus* and is generally less than half the length of II (figs. 8, 9). Trichobothria on basitarsi of legs with **sbc** slightly more basad than **sbf** and nearer to **sbf** than to **stf**; **sbc** approximately equidistant between **bf**₁ and **stf** (fig. 7). In the other species of *Paraphrynus* **sbc** is much closer to **stf** than **sbf**.

Description:—Anterior edge of carapace straight (fig. 6). Surface finely granular with greatest density of granules in ocular area, becoming more scattered posteriorly. A few coarser setiferous granules located over entire surface becoming inconspicuous in ocular area. Lacking median and lateral eyes.



Figs. 1-7.—*Paraphrynus reddelli*: 1, right pedipalp femur, dorsal view; 2, right pedipalp tibia, dorsal view; 3, left pedipalp femur, ventral view; 4, left pedipalp tibia, ventral view; 5, left pedipalp basitarsus, inner lateral view; 6, anterior edge of carapace; 7, left basitarsus of leg IV showing patterns of trichobothria.

Figs. 8-9.—*Paraphrynus* sp. showing presence of spine I: 8, right pedipalp tibia, dorsal view; 9, left pedipalp tibia, ventral view.

Dorsal surface of pedipalp femur with 10 spines (fig. 1). Ventral surface with 12 spines (fig. 3); setae extending length of spines I and II; between II and III is a well developed spine greater than half the length of II and slightly shorter than III. Dorsal surface of pedipalp tibia with 11 spines (fig. 2); this surface lacking a spine corresponding to I thereby making the actual second spine (III) longest; between VI and VII is a well developed spine only slightly shorter than VII and longer than VIII. Ventral surface of pedipalp tibia with 14 spines (fig. 4); this surface also lacks a spine corresponding to I; with 2 spines between IV and V and 2 more between V and VI, the longest between V and VI is considerably longer than half the length of VI. Pedipalp basitarsus with 8 dorsal and 8 ventral spines (fig. 5).

Measurements: *Carapace*; median length 4.2 mm, width 5.6 mm. *Pedipalps*; length of femur 3.2 mm, width of femur 0.8 mm, length of tibia 4.0 mm, width of tibia 0.8 mm, length of longest dorsal tibial spine (III) 1.6 mm, length of basitarsus 2.4 mm, length of tarsus 2.2 mm. *Leg I* femur 12.2 mm; *Leg II* femur 8.4 mm, tibia 7.6 mm, basitarsus 5.2 mm, tarsus 1st segment 1.4 mm, 2nd segment 0.5 mm, 4th segment 0.6 mm. *Leg III* femur 9.4 mm, tibia 8.8 mm, basitarsus 6.0 mm, tarsus 1st segment 1.4 mm, 2nd segment 0.5 mm, 3rd segment 0.6 mm. *Leg IV* femur 8.0 mm, tibia 1st segment 4.8 mm, 2nd segment 0.6 mm, 3rd segment 2.8 mm, tarsus 1st segment 1.4 mm, 2nd segment 0.5 mm, 4th segment 0.6 mm. *Abdomen*; length 6.8 mm, female genital operculum length 1.2 mm, width 2.4 mm.

Distribution:—Known only from type locality.

Material Examined:—The types, and 2 immature specimens, 1 male and 1 undetermined sex.

Etymology:—The species is named in honor of James Reddell, one of the collectors of the type specimens who has participated in extensive collecting of cave arthropods in Mexico.

Comments:—Numbering of spines is according to that used in the last revision for the genus (Mullinex, C.L.1975.Occ. Papers California Acad. Sci., N^o 116, 80 pp.). The actual number of spines is considered less important than the presence of certain spines. Therefore in *P. reddelli* not all spines have been given numbers. However those spines considered homologous to major spines found in other species of *Paraphrynus* have been given corresponding roman numerals. In an individual, the actual number of spines on any one surface of a pedipalp segment may differ slightly from the numbers given in the description.

Labeling of trichobothria is according to P. Weygoldt (1970. Z. Morph. Tiere, 67: 58-85).

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THE JOURNAL OF ARACHNOLOGY

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4

3

The following special directions apply to authors of taxonomic papers:

(a). Do not use abbreviations to indicate that a new name or a new combination is being proposed in a primary heading (e. g., *A-us x-us*, new species, rather than *A-us x-us*, n. sp. or comparable abbreviations).

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A-us x-us Jones 1930:3, 1935:9; Russell 1945:453; Smith 1954a:16, 1954b:678; Cooper and Lim 1955:18 (in part).

A-us y-us Bates 1932:18, fig. 4. NEW SYNONYMY.

A-us z-us: Miranda 1948:98 (misidentification); Harris 1951:3 (in part ?). (*nec A-us z-us* Zimmer

(d). Lists of specimens examined of a given taxon must be the last item typed in the treatment of that taxon as they will be set in smaller type. Adhere to the following style for listing specimens examined: Country: state or comparable political subdivision; county or district, detailed locality (elevation), 14 July 1945 (collector), 2 males, 5 females (acronym of institution where specimens are deposited), next detailed locality within that county, and so forth; next county in the same state; and so forth: next state in the same country; and so forth. Next country: and so forth. Punctuation rules are very simple. Use a period to separate countries, colon to separate states, semi-colon to separate counties, and commas to separate specific localities.

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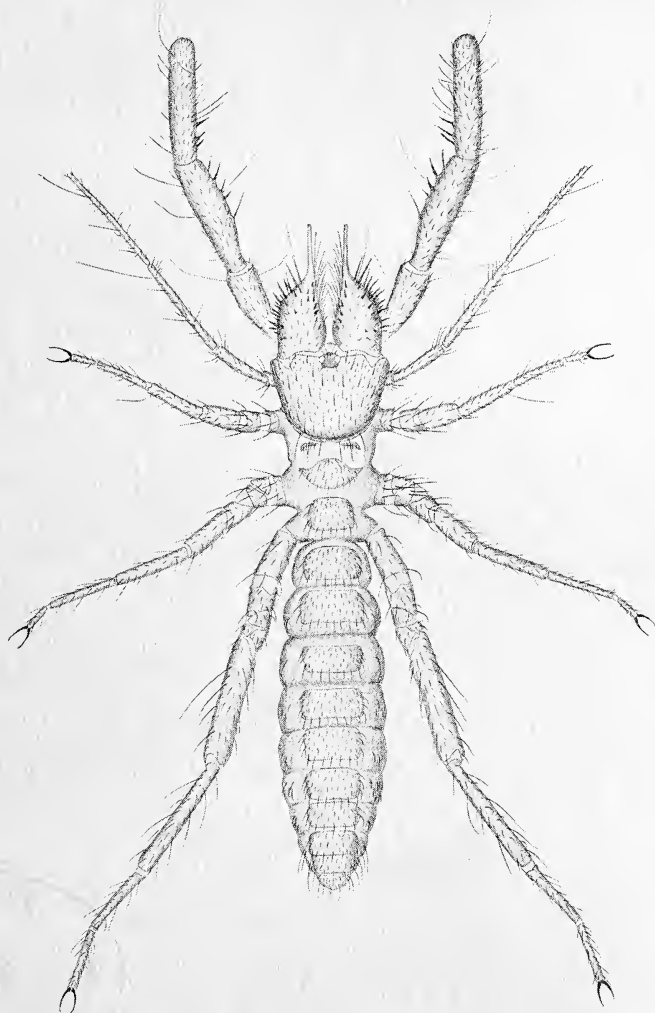
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THE ORDER SCHIZOMIDA (ARACHNIDA) IN THE NEW WORLD. III. *MEXICANUS* AND *PECKI* GROUPS (SCHIZOMIDAE: *SCHIZOMUS*)¹

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ABSTRACT

A systematic revision of the *Schizomus mexicanus* and *S. pecki* species groups (Arachnida, Schizomida, Schizomidae) is presented. The following species are described and assigned to the *mexicanus* group: *S. mulaiki* Gertsch, *S. bartolo* Rowland, *S. lukensi* Rowland, *S. davisii* Gertsch, *S. reddelli* Rowland, *S. mexicanus* Rowland, *S. pallidus* Rowland, *S. portoricensis* (Chamberlin), *S. moisii* Rowland, *S. cookei* Rowland, and *S. mitchelli* Rowland. Three taxa known only from females (*Schizomus* spp., OTU Nos. 1, 2, and 11) are also briefly described and assigned to the *mexicanus* group. The following species are described and assigned to the *pecki* group: *S. firstmani* Rowland, *S. sp. cf. sbordonii* Brignoli, *S. pecki* Rowland, and *S. guatemalensis* Chamberlin. Brief descriptions are also provided for four taxa assigned to the *pecki* group that are known only from females (*Schizomus* spp., OTU Nos. 2, 6, 7 and 8).

INTRODUCTION

This is the third part of a revision of the arachnids of the order Schizomida in the New World. The first part (Rowland and Reddell 1979a) included the family Protoschizomidae and the *Schizomus dimitrescoae* group of the family Schizomidae. The second part included the primarily South American *Schizomus simonis* and *S. brasiliensis* groups (Rowland and Reddell 1979b). The present report includes a revision of the largely Mexican *Schizomus mexicanus* and *S. pecki* groups. Table 1 may be used to compare the species groups included here with the remaining groups of New World schizomids. Uniform descriptions are included for all species, and include all characters which have been found to be of value in distinguishing taxa (see Rowland and Reddell 1979a for a discussion of the characters used). A fourth report will cover the remaining New World schizomids. A detailed discussion of the zoogeography and phylogeny will follow the systematic revision of the order.

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As in the previous report (Rowland and Reddell 1979b) several species are briefly described for which males are not known. These taxa are not named, but are included because they are of value in analyzing the phylogenetic and zoogeographic relationships within the order (see Rowland and Reddell 1979a, 1979b).

The present study is based to a large extent on a dissertation prepared by the senior author at Texas Tech University, Lubbock, Texas (Rowland, 1975a).

Family Schizomidae

MEXICANUS GROUP

Description.—Members of this group are moderate to large in size (0.98-1.44 mm carapacial length). The color is usually brownish but green species occur. Eyespots are present in epigean species, but are usually indistinct and ovoid with diffuse margins; they are frequently absent in cavernicoles. The carapace has two or three pairs of dorsal and two apical setae. Males: abdomen never elongate; abdominal process absent; flagellum usually small, ovate, and dorsally compressed; dorsal surface usually bears a pair of lateral depressions. Females: flagellum short and composed of three articles; spermathecae generally characterized by an enlargement of the median pair and reduction of the laterals; some species lack the laterals altogether, but in some they are nearly as large as the medians; a few species have terminal enlargements. The pedipalps sometimes are highly sexually dimorphic, but sometimes variably so. In species with dimorphic pedipalps an elaboration of all segments and production of a tibial spur apposable to the tarsus-basitarsus is characteristic; however, individuals with only slightly dimorphic pedipalps do not express the spur.

Distribution.—Excluding *Schizomus portoricensis*: United States: Texas. México: Nuevo León, Tamaulipas, San Luis Potosí, Guerrero Veracruz, Oaxaca, Chiapas. *S. portoricensis*: Bermuda, Florida, Antilles, southern México. Central America, northern South America, Galapagos Islands.

Remarks.—*Schizomus antilus* Hilton 1933, from Cuba has not been studied by us. The types, reportedly deposited in the Pomona College, California, Museum, have not been located. Based on measurements given in the original description, *S. antilus* is probably a junior synonym of *S. portoricensis*. See Table 2 for comparisons of the species in the *mexicanus* group.

Subordinate taxa.—Unnamed complex: OTU No. 1, Otu No. 2; *Mexicanus* complex: *S. mulaiki*, *S. bartolo*, *S. lukensi*, *S. davisi*, *S. reddelli*, *S. mexicanus*; *portoricensis* complex: *S. pallidus*, *S. portoricensis*; *moisii* complex: OTU No. 11, *S. moisii*; *mitchelli* complex: *S. cookei*, *S. mitchelli*.

Schizomus sp., OTU No. 1

Figs. 1, 45

Schizomus sp.: Reddell 1971a:219 [Grutas de Cacahuamilpa record only].

Schizomus sp. 1: Rowland and Reddell 1977:80, 84, 96.

Description.—Female. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots absent. Anterior sternum with 11 bifid setae. Abdominal terga I-VIII with two setae, tergum IX with four setae. Vestigial stigmata darker than sterna.

Flagellum composed of three articles. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 43-5-8-10-11-10-20. Other leg segment measurements given in Table 3. Median and lateral spermathecae slightly divergent, the medians somewhat larger, medians and laterals with variable, slightly sclerotized bulbs.

Male unknown.

Specimens examined.—Female and immature taken in Grutas de Cacahuamilpa, Guerrero, México, 15 August 1966 (J. Fish and J. Reddell) (TTU).

Comparisons.—See under *Schizomus* sp., OTU No. 2.

Distribution.—Known only from Grutas de Cacahuamilpa, Guerrero, México.

Table 1.--Comparisons of the New World species groups of the genus *Schizomus*. See Rowland and Reddell (1979) for explanation of characters.

CHARACTER	dumitres-coae	simonis	brasil-iensis	mexi-canus	pecki	goodni-ghtorum	briggsi
DORSAL SETAE	2-3	2-3	3-4	2-3	2-3	3-4	3-4
METAPEL-TIDIUM	entire	entire	split or entire	entire	entire	entire	split or entire
COLOR	brown or green	brown or green	brown or green	brown or green	brown	brown	brown or green
SPERMA-THECAE	M < L	M < L	M = L	M > L	M > L	M > L	multiple
ART. FEM. FLAGELLUM	4	4	3	3	3	3	4
CARAPACE LENGTH	.96-1.37	1.07-1.34	.91-1.48	.98-1.37	1.31-1.74	.89-1.42	1.18-1.52
ABDOMINAL ELONGATION	none	present	none	none	none	present	none or present
ABDOMINAL PROCESS	present	present	present	absent	absent	absent	present
PEDIPALPAL DIMORPHISM	slight to strong	none	slight to strong	none to strong	none	none	none to strong
SHAPE MALE FLAGELLUM	bulbous	long	bulbous	bulbous	bulbous	long	long or bulbous

Schizomus sp., OTU No. 2

Figs. 1, 41

Description.—Female. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots distinctly triangular. Anterior sternum with nine entire setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum composed of three articles. Pedipalpal trochanter slightly produced distally; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 31-4-5-6-5-6-15. Other leg segment measurements given in Table 3. Median spermathecae about 1/4 longer than laterals, both pair straight, slightly divergent, each with apical portions sclerotized.

Male unknown.

Specimens examined.—Female and immature taken 20 mi S. Juchatengo (6000 ft.), Oaxaca, México, 29 May 1971 (S. Peck) (TTU).

Comparisons.—This species appears to be closely related to OTU No. 1, but in OTU No. 2 the flagellum is shorter and the median spermathecae are nearly straight and have thicker apical spermathecal walls. The presence of only two setae on abdominal terga VIII, rather than four, separates this species from all other members of the *mexicanus* group.

Distribution.—Known only from 20 mi. S. Juchatengo, Oaxaca México.

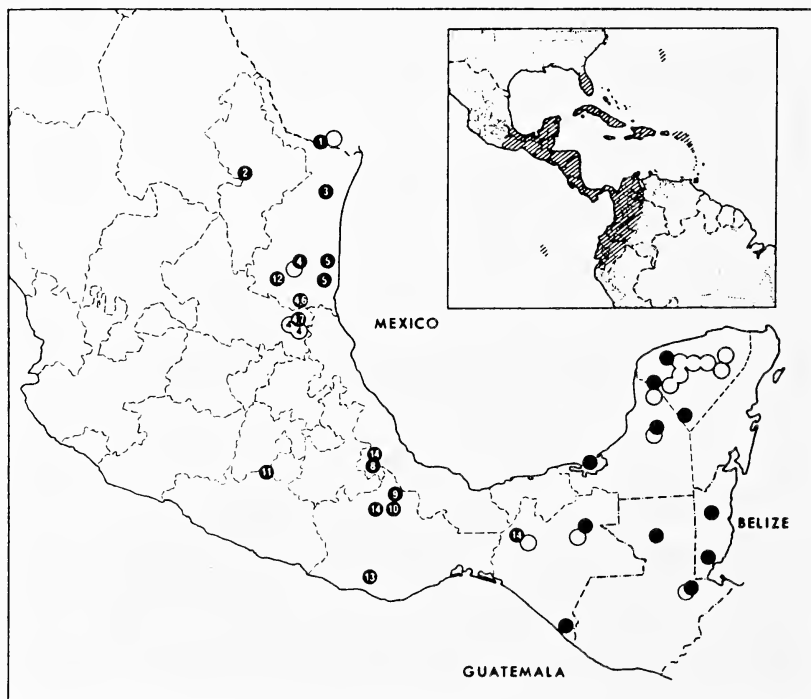


Fig. 1.—Map showing distribution of schizomids of the *mexicanus* group: 1, *S. mulaiki*; 2, *S. bartolo*; 3, *S. davisi*; 4, *S. mexicanus*; 5, *S. lukensi*; 6, *S. mitchelli*; 7, *S. cookei*; 8, *S. pallidus*; 9, *S. moisii*; 10, OTU No. 11; 11, OTU No. 1; 12, *S. reddelli*; 13, OTU No. 2; 14, unnumbered solid circles and inset, *S. portoricensis*.

Table 2.-Comparisons of members of the *mexicanus* group. See the introduction to Rowland and Reddell (1979a) for discussion of characters.

CHARACTER	OTU #1	OTU #2	mulaiki	bartolo	lukensi	davisi	reddelli	mexicanus	pallidus	portor- icensis	OTU #11	moisii	cookei	mittchelli
DORSAL SETAE	2	2	2	3	3	2	2	2	3	2	3	3	3	3
STERNAL SETAE	11	9	12	11	9	13	10	10	11	9	9	9	11	11
COLOR	brown	brown	brown	brown	brown	brown	brown	brown	brown	green or brown	green	green	brown	brown
PEDIPALPAL DIMORPHISM	?	?	none?	slight	slight	none?	none	none to strong	slight	none to slight	?	slight	strong	strong
EYESPOTS	absent	distinct	indis- tinct	absent	absent	indis- tinct	absent	indis- tinct	indis- tinct	indis- tinct to distinct	distinct	distinct	absent	absent
SPERMA- THECAE	M ± L	M ± L	?	M 2X L	M 10X Lor laterals absent	?	laterals absent	M 1-2X L	M 2X L	M ±2x L	M 9X L	M 3X L	multiple	multiple
CARAPACE LENGTH	1.14	1.14	.98	1.04	1.34	1.18	1.13	1.11	1.44	1.07	.99	1.13	1.23	1.22
LENGTH FEM. FLAGELLUM	.37	.25	?	.28	.35	?	.30	.30	.45	.26	.24	.26	.37	.33
PIT MALE FLAGELLUM	?	?	single	absent	absent	double	double	double	double	double	?	double	single	single

Schizomus mulaiki Gertsch

Figs. 1, 8, 25

Schizomus mulaiki Gertsch 1940:1, 3-4; Rowland 1971b:304; Rowland and Reddell 1976:3; Rowland and Reddell 1977:79, 83.

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with 12 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of postero-dorsal process. Vestigial stigmata darker than sterna. Flagellum nearly circular, the body wider than long, with a distal median depression. Pedipalpal trochanter not produced distally; tarsal-basitarsal spurs about $1/6$, claw about $1/3$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 26-5-5-6-7-7-18. Other leg segment measurements given in Table 3.

Female unknown.

Type data.—Holotype male taken at Rio Grande City, Starr County, Texas, 21 June 1939 (S. Mulaik) (AMNH, examined); paratype male taken at Edinburg, Hidalgo County, Texas, 2 June 1935 (S. Mulaik) (AMNH, examined).

Comparisons.—*S. mulaiki* is very similar to other members of the *mexicanus* complex. It is distinct in having a small, single apical depression on the male flagellum. All other males within the group have either no dorsal relief or have a pair of distal depressions.

Distribution.—Known only from Hidalgo and Starr Counties in the Rio Grande Valley of Texas.

Remarks.—The morphology of the male flagellum was probably a result of a central fusion of the ancestral pair of depressions. A slight proximal cleavage of the pit is still apparent. Although this species is known only from the two type specimens, Stanley Mulaik (pers. comm.) stated that he has seen it all along the Rio Grande, perhaps 100 miles northwest of the type locality.

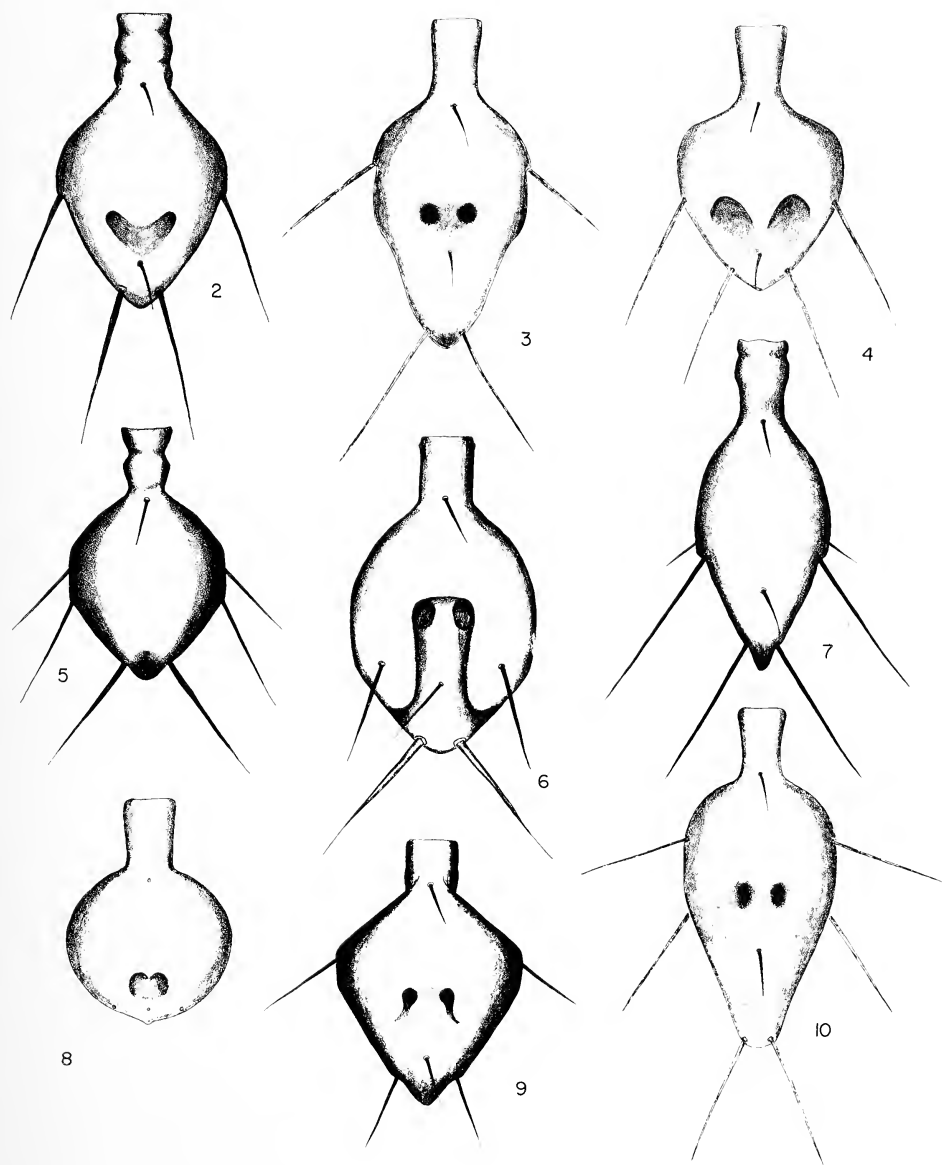
Schizomus bartolo Rowland

Figs. 1, 5, 21, 40

Schizomus sp.: Reddell 1967a:25; Reddell 1971b:28 [Grutas de San Bartolo record only].
Schizomus bartolo Rowland 1973a:13-16, 18; Rowland 1973c:135, 137; Dumitresco 1977:157; Rowland and Reddell 1977:80, 83, 84.

Description.—Male. Color pale brown. Carapace with three pairs of dorsal, the medians being very small, and two apical setae. Eyespots absent. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum globose, with no dorsal relief. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about $1/4$, claw about $1/2$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 38-7-7-7-10-9-20. Other leg segment measurements given in Table 3.

Female. Flagellum composed of three articles. Median spermathecae large, straight, wide, slightly convergent; laterals smaller, convergent and constricted into divergent curves apically, the medians apically sclerotized.



Figs. 2-10.—Dorsal views of male flagella of the *mexicanus* group: 2, 3, *S. mexicanus*: 2, from the type locality; 3, from Gómez Farías; 4, *S. davisi*; 5, *S. bartolo*; 6, *S. portoricensis* from Cueva Cerro Hueco, Chiapas; 7, *S. lukensi*; 8, *S. mulaiki*; 9, *S. moisii*; 10, *S. reddelli*.

Table 3.—Measurements (mm) of six species of the *mexicanus* group: 1, one female, OTU No. 1; 2, one female, OTU No. 2; 3, one male, *S. mulaiki*; 4, one male, *S. bartolo*; 5, one female, *S. bartolo*; 6, one male, *S. lukensi*; 7, one female, *S. lukensi*; 8, one male, *S. davisii*. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6	7	8
Carapace	1.14	1.14	0.98	0.99	1.04	1.14	1.34	1.18
Flagellum								
Length	0.37	0.25	0.26	0.33	0.28	0.45	0.35	0.35
Width	—	—	0.22	0.21	—	0.18	—	0.23
Leg I								
Femur	1.46	0.86	0.90	1.16	1.09	1.50	1.30	1.03
Patella	1.70	0.97	1.08	1.47	1.41	1.94	1.16	1.29
Tibia	1.28	0.73	0.83	1.13	1.11	1.49	1.25	0.97
Tarsus-Basitarsus	1.07	0.72	0.74	0.95	0.86	0.97	1.00	0.83
Leg II								
Femur	0.97	0.65	0.62	0.70	0.68	0.90	0.90	0.73
Patella	0.49	0.39	0.36	0.38	0.32	0.32	0.41	0.45
Tibia	0.50	0.40	0.40	0.50	0.53	0.57	0.62	0.46
Basitarsus	0.52	0.37	0.35	0.43	0.37	0.51	0.45	0.41
Leg III								
Femur	0.86	0.61	0.56	0.63	0.60	0.79	0.78	0.64
Patella	0.40	0.25	0.25	0.27	0.28	0.35	0.34	0.33
Tibia	0.57	0.32	0.33	0.41	0.38	0.53	0.53	0.36
Basitarsus	0.61	0.39	0.37	0.47	0.38	0.54	0.53	0.43
Leg IV								
Femur	1.31	0.97	0.84	1.05	1.00	1.22	1.19	0.97
Patella	0.47	0.44	0.35	0.35	0.36	0.47	0.42	0.46
Tibia	1.00	0.63	0.61	0.78	0.77	0.90	0.81	0.72
Basitarsus	0.93	0.58	0.52	0.68	0.68	0.79	0.74	0.60

Type data.—Holotype male, allotype female, and eight paratype immatures taken in Grutas de San Bartolo, 10 mi. SW Monterrey, Nuevo León, México, 21 June 1969 (S. and J. Peck) (AMNH, examined); four paratype females taken in Grutas de San Bartolo, September 1971 (T. Raines, TTU, examined).

Comparisons.—See under *S. lukensi*.

Distribution.—Known only from Grutas de San Bartolo, Nuevo León, México.

Remarks.—This species is apparently a troglobite now isolated in Grutas de San Bartolo by the surrounding desert. Grutas de San Bartolo is a name applied to two adjacent caves, designated as Sur and Norte. It is not known from which cave the type series was taken.

Additional record.—*Nuevo León*: Gruta Sur de San Bartolo, February 1966 (B. Russell), four females, four immatures (AMNH).

Schizomus lukensi Rowland

Figs. 1, 7, 20, 38-39

Schizomus lukensi Rowland 1973c:136-137; Rowland 1975b:19, 20; Dumitresco 1977:157; Rowland and Reddell 1977:80, 83-84.

Description.—Male. Color pale brownish. Carapace with three pairs of dorsal and two apical setae. Eyespots absent. Anterior sternum with nine bifid setae. Abdominal terga

I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata lighter than sterna. Flagellum lanceolate, with no dorsal relief. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 41-7-9-8-9-10-22. Other leg segment measurements given in Table 3.

Female. Flagellum composed of three articles. Spermathecae with medians extremely long, divergent, with slight terminal bulbs, only one very small lateral present.

Type data.—Holotype male, allotype female, and two male and two female paratypes taken in Cueva del Agua, 30 mi. SW Soto la Marina, Tamaulipas, México, 31 October 1970 (W. Russell, G. Ediger, J. Ediger) (AMNH, examined).

Comparisons.—*S. lukensi* shares with *S. bartolo* the possession of three pairs of dorsal carapacial setae and lack of dorsal relief on the male flagellum. The male flagellum, however, is longer and narrower in *S. lukensi* than in *S. bartolo*. Females of *S. lukensi* have only very small lateral spermathecae, whereas those of *S. bartolo* are well developed.

Distribution.—Known only from two caves in the Sierra de Tamaulipas, Tamaulipas, México.

Remarks.—Specimens from Cueva de los Cuarteles, near Aldama, Tamaulipas, México, are very similar to *S. lukensi* (Fig. 39). The female spermathecae differ, however, in completely lacking the laterals. The male flagella, also, show slight but consistent differences between the two populations and they probably should be considered distinct species.

Additional record.—*Tamaulipas*: Cueva de la Virgen de Guadalupe, 48 km SW Soto la Marina, 31 October 1970 (W. Russell, G. Ediger, J. Ediger), 1 female (TTU).

Schizomus davis Gertsch

Figs. 1, 4, 24, 58

Schizomus davis Gertsch 1940:1-4; Rowland 1971a:117; Rowland 1973a:21; Rowland 1973c:135; Brignoli 1974:149; Rowland and Reddell 1977:83.

Description.—Male. Color brownish. Carapace with three pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with 13 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII without evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum spade shaped, with a pair of deep depressions undercutting a dorsal medially produced ridge. Pedipalpal trochanter produced apically into a tubercle which bears an apical spine; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 28-6-7-6-8-9-19. Other leg segment measurements given in Table 3.

Female unknown.

Type data.—Holotype male taken at San Fernando, Tamaulipas, México 28 March 1937 (L. Irby Davis) (AMNH, examined).

Comparisons.—*S. davis* is closely related to *S. mexicanus* and *S. mulaiki*. It may be readily distinguished from *S. mulaiki* by the presence of one small distal depression in *S. mulaiki* rather than two depressions. The distal pits are better defined in *S. davis* than in *S. mexicanus*. The pedipalps of *S. davis* are shorter and thicker than are those of *S. mexicanus* and the trochanter of *S. davis* has an apical spine absent in *S. mexicanus*.

Table 4.—Measurements (mm) of four species of the *mexicanus* group: 1, one male, *S. reddelli*; 2, one female, *S. reddelli*; 3, nine males, *S. mexicanus*; 4, 12 females, *S. mexicanus*; 5, two males, *S. pallidus*; 6, one female, *S. pallidus*; 7, one female, OTU No. 11. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6	7
Carapace	1.12	1.13	1.14–1.28	1.20–1.31	1.21–1.37	1.44	0.99
Flagellum							
Length	0.49	0.30	0.39–0.40	0.31–0.35	0.49–0.53	0.45	0.24
Width	0.20	—	0.20–0.22	—	0.25–0.26	—	—
Leg I							
Femur	1.13	1.02	1.23–1.39	1.10–1.20	1.64–1.86	1.73	0.85
Patella	1.57	1.26	1.43–1.71	1.33–1.42	2.11–2.12	2.08	0.97
Tibia	1.13	0.90	1.05–1.61	0.94–1.02	1.52–1.53	1.60	0.71
Tarsus-Basitarsus	1.02	0.81	0.92–0.97	0.84–0.97	1.20–1.22	1.11	0.67
Leg II							
Femur	0.82	0.73	0.90–0.97	0.82–0.86	1.07–1.09	1.15	0.59
Patella	0.40	0.41	0.49–0.54	0.45–0.48	0.52–0.59	0.63	0.34
Tibia	0.59	0.47	0.62–0.67	0.55–0.59	0.80–0.80	0.80	0.35
Basitarsus	0.48	0.39	0.48–0.52	0.43–0.49	0.55–0.58	0.62	0.35
Leg III							
Femur	0.70	0.64	0.80–0.82	0.74–0.89	0.97–0.99	1.06	0.54
Patella	0.29	0.30	0.31–0.40	0.35–0.49	0.46–0.61	0.45	0.23
Tibia	0.44	0.37	0.47–0.50	0.42–0.59	0.59–0.78	0.62	0.26
Basitarsus	0.48	0.44	0.54–0.58	0.48–0.51	0.63–0.65	0.68	0.35
Leg IV							
Femur	1.05	1.02	1.22–1.30	1.15–1.21	1.50–1.53	0.81	0.87
Patella	0.38	0.40	0.52–0.59	0.50–0.54	0.60–0.64	0.62	0.41
Tibia	0.81	0.71	0.89–0.92	0.78–0.87	1.09–1.11	1.21	0.57
Basitarsus	0.75	0.62	0.77–0.82	0.70–0.76	0.93–0.95	1.00	0.54

Distribution.—known only from the type locality.

Remarks.—This species is probably a relict of a once widely distributed common ancestor of *S. mexicanus*, *S. reddelli*, *S. lukensi*, *S. bartolo*, and *S. mulaiki*. The specimen was probably collected near the banks of the Río San Fernando, since other areas surrounding San Fernando seem quite xeric and thus unsuited for schizomids.

Schizomus reddelli Rowland

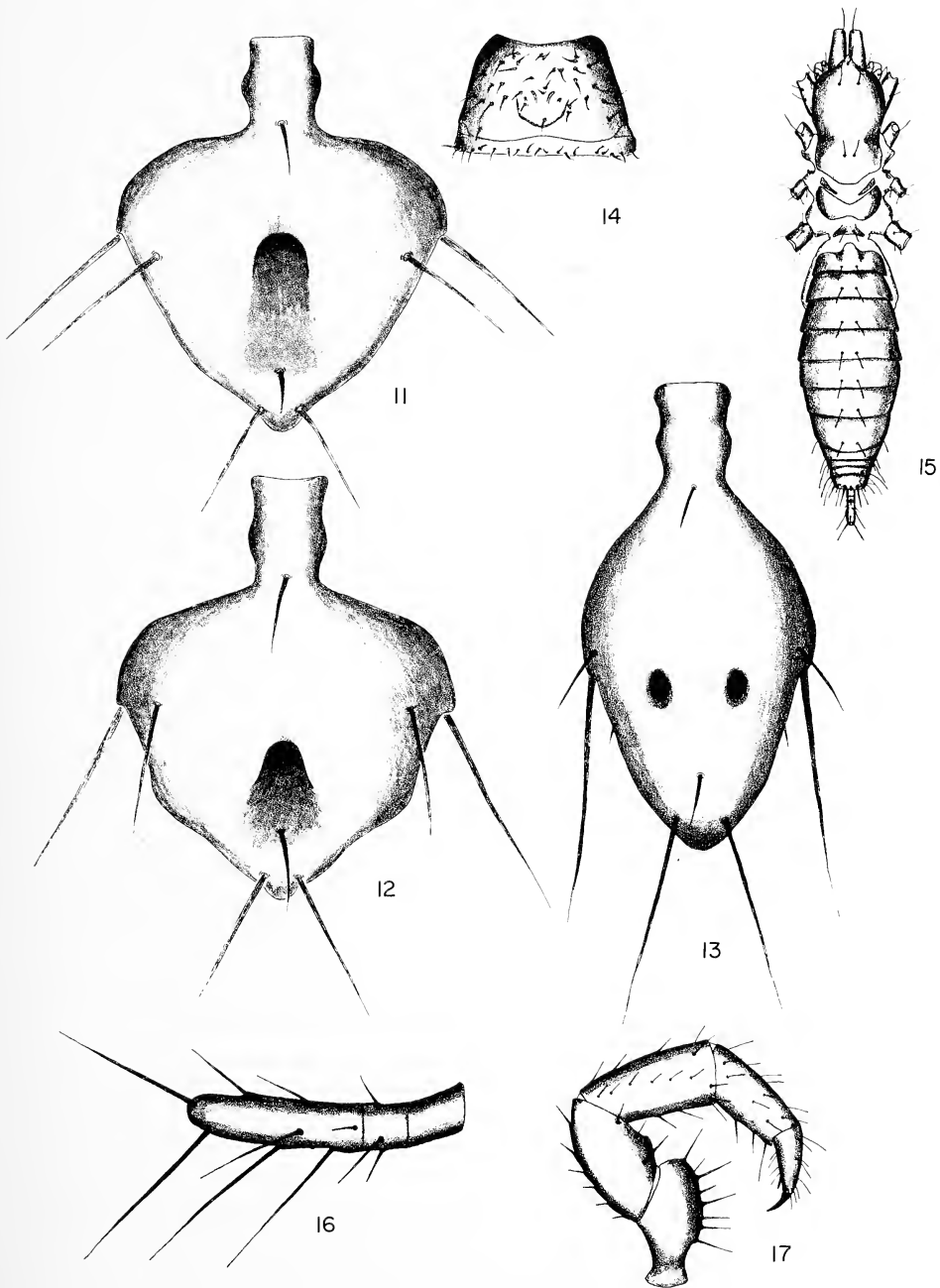
Figs. 1, 10, 22, 36-37

Schizomus reddelli Rowland 1971a:123, 124, 126; Reddell and Mitchell 1971b:185; Rowland 1973a:21; Rowland 1973c:135; Reddell 1973:38; Brignoli 1974:147, 149; Rowland and Reddell 1977:80, 84, 85.

Schizomus mexicanus: Reddell and Mitchell 1971b:185 [misidentification]; Vomero 1974:341 [misidentification].

Schizomus reddeli: Dumitresco 1977:157 [erroneous spelling].

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots absent or only very indistinct. Anterior sternum with 10 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII without evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum



Figs. 11-17—Parts of schizomids of the *mexicanus* group: 11-13, dorsal views of male flagella: 11, *S. mitchelli*; 12, *S. cookei*; 13, *S. pallidus*; 14-17, female *S. portoricensis*: 14, ventral view of abdominal sterna II and III, showing spermathecae through the integument; 15, dorsal view, legs and pedipalps past the trochanter omitted; 16, lateral view of flagellum; 17, lateral view of right pedipalp.

lanceolate, with faint depressions medially, nearly flat dorsally. Pedipalpal trochanter produced slightly distally; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 37-7-9-8-10-10-20. Other leg segment measurements given in Table 4.

Female. Flagellum composed of three articles. Lateral spermathecae missing; medians long, thin, and slightly curved outward.

Type data.—Holotype male taken in Cueva de Tres Manantiales, 8 km NNE Chamal, Tamaulipas, México, 27 May 1968 (J. Reddell) (AMNH, examined); allotype female taken in Cueva de Tres Manantiales, January 1972 (W. Russell) (TTU, examined).

Comparisons.—*S. reddelli* is generally larger than *S. mexicanus*. Females of *S. reddelli* have a single pair of spermathecae, while those of *S. mexicanus* have both pair. While the morphology of the male flagellum in *S. mexicanus* is, in most cases, distinct from *S. reddelli*, a variant from near Gómez Farías, Tamaulipas, shows striking similarity to that of *S. reddelli*. See also under *S. mexicanus*.

Distribution.—Known only from two caves near Chamal, Tamaulipas, México.

Remarks.—Although the male flagellum is usually the best character to be used in species recognition, the similarity of the flagella of a population of *S. mexicanus* from Gómez Farías to that of typical *S. reddelli* makes this character less reliable than the female spermathecae in distinguishing these two closely related species. *S. reddelli* is probably a high altitude relict of a formerly widely ranging population ancestral to it and *S. mexicanus*. This species is probably now restricted to the cave environment.

Additional records.—*Tamaulipas*: Cueva de Tres Manantiales, January 1972 (W. Russell), one female, one immature (TTU); Cueva de los Vampiros, 6 mi. NNE Chamal, 27 May 1968 (J. Reddell), one male, three females, five immatures (TTU).

Schizomus mexicanus Rowland

Figs. 1-3, 18-19, 32-34, 54-57

Schizomus sp.: McKenzie 1965:35, 37; Reddell 1967b:82; Reddell 1971b:28 [Cueva Grande and Ventana Jabalí records only]; Reddell and Mitchell 1971a:145; Reddell and Elliott 1973:183.

Schizomus mexicanus Rowland 1971a:117-119; Reddell and Mitchell 1971a:145; Rowland 1973a:10, 21, 22; Rowland 1973b:200-201; Rowland 1973c:135, 137; Brignoli 1973:6; Reddell 1973:38; Reddell and Elliott 1973:183; Brignoli 1974:143, 146-147, 149, 151; Vomero 1974:341, 345; Rowland 1975b:15, 19, 20; Rowland and Reddell 1977:80, 83, 85, 86, 87, 96.

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with 10 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of postero-dorsal process. Vestigial stigmata darker than sterna. Flagellum ovoid, with a pair of subdistal pits. Pedipalpal trochanter produced apically slightly; other segments elongate; the tibia with a jutting spur apposable to the tarsus-basitarsus; tarsal-basitarsal spurs about 1/5, claw about 1/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 45-8-10-9-10-10-27. Other leg segment measurements given in Table 4.

Female. Flagellum composed of three articles. Median and lateral spermathecae outwardly divergent, medians somewhat larger than laterals, slightly expanded and sclerotized apically.

Type data.—Holotype male, allotype female, and paratype male and female taken in Sótano de la Tinaja, 10 km NNE Ciudad Valles, San Luis Potosí, México, 18 February 1970 (J. A. L. Cooke) (AMNH, examined).

Comparisons.—*S. mexicanus* is most closely related to *S. reddelli* and *S. davisii*. The trochanter of the pedipalp of the male of *S. davisii* is greatly produced, whereas it is only slightly produced in *S. mexicanus*. The dorsal depressions on the male flagellum are more distinct and proximal in *S. davisii* than in *S. mexicanus*. The flagellum of the male of *S. reddelli* is longer than that of typical *S. mexicanus*. *S. reddelli* also lacks definition of a median depression, but a population of *S. mexicanus* from near Gómez Farías, Tamaulipas, also lacks a well-defined median depression. Females of *S. reddelli* lack the lateral spermathecae, which are always present in *S. mexicanus*.

Distribution.—*S. mexicanus* occurs in epigeal and subterranean habitats in the Sierra de El Abra, San Luis Potosí and Tamaulipas; and in the Sierra de Guatemala, Tamaulipas.

Variation.—Two males from the Gómez Farías roadcut have an elongated flagellum unlike that observed elsewhere in the range of the species. Females from the same locality are identical to those from the type locality. The pedipalps of the male are strongly sexually dimorphic in cave populations, but are more similar in epigeal populations.

Additional records.—See Rowland and Reddell (1977) for other records.

Schizomus pallidus Rowland

Figs. 1, 13, 26, 43

Schizomus pallidus Rowland 1975b:7, 13-15, 17; Rowland and Reddell 1977:80, 84, 87, 88, 89.

Description.—Male. Color pale brownish. Carapace with three pairs of dorsal, the medians very small, and two apical setae. Eyespots indistinct. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum lanceolate, with a pair of median depressions. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 56-10-12-10-11-12-26. Other leg segment measurements given in Table 4.

Female. Flagellum composed of three articles. Median and lateral spermathecae divergent, the medians about twice as long as laterals; both pairs evenly sclerotized along length.

Type data.—Male holotype and female allotype taken in Cueva Macinga, Tlilapan, Veracruz, México, 5 March 1973 (J. Reddell) (AMNH, examined); one male, two female, and two immature paratypes taken with the holotype (TTU, examined).

Comparisons.—See under *S. portoricensis*.

Distribution.—Known only from the type locality.

Remarks.—The large size and reduction of pigmentation in this species indicates that it is probably a troglobite which has not yet completely lost the eyespots. Specimens were taken from beneath rocks on silt in a small side passage.

Additional record.—Veracruz: Cueva Macinga, 9 January 1977 (J. Reddell, A. Grubbs, D. McKenzie, C. Soileau), 1 female, 3 immatures (TTU).

Schizomus portoricensis (Chamberlin)

Figs. 1, 6, 14-17, 28, 46-53.

Stenochrus portoricensis Chamberlin 1922:11-12; Mello-Leitão 1931:19; Giltay 1935:8; Werner 1935:469; Takashima 1943:93; Rowland 1973b:195, 197, 200; Brignoli 1974:145.

Schizomus antilus Hilton 1933:91-92; Giltay 1935:6; Takashima 1943:94. **Possible synonymy.**

Schizomus cavernicolens Chamberlin and Ivie 1938:102, 103; Gertsch 1940:4; Takashima 1943:94; Pearse 1945:153; Cárdenas Figueroa 1950:154; Nicholas 1962:181; Vandel 1964:116; Vandel 1965:93; Reddell 1971b:28; Rowland 1971a:117; Brignoli 1974:149; Reddell, 1977:230.

Schizomus probably *latipes* Hansen (in Hansen and Sörensen): Cloudsley-Thompson 1949:261 [misidentification].

Schizomus floridanus Muma 1967:18-20; Rowland 1971b:304.

Schizomus longimanus Rowland 1971a:118-120; Reddell 1973:38; Rowland 1973a:13; Rowland 1973c:135, 137; Brignoli 1973:6, 7, 8, 9; Brignoli 1974:143, 144, 146, 147, 151; Rowland 1975b:15, 17, 19, 20; Dumitresco 1977:157.

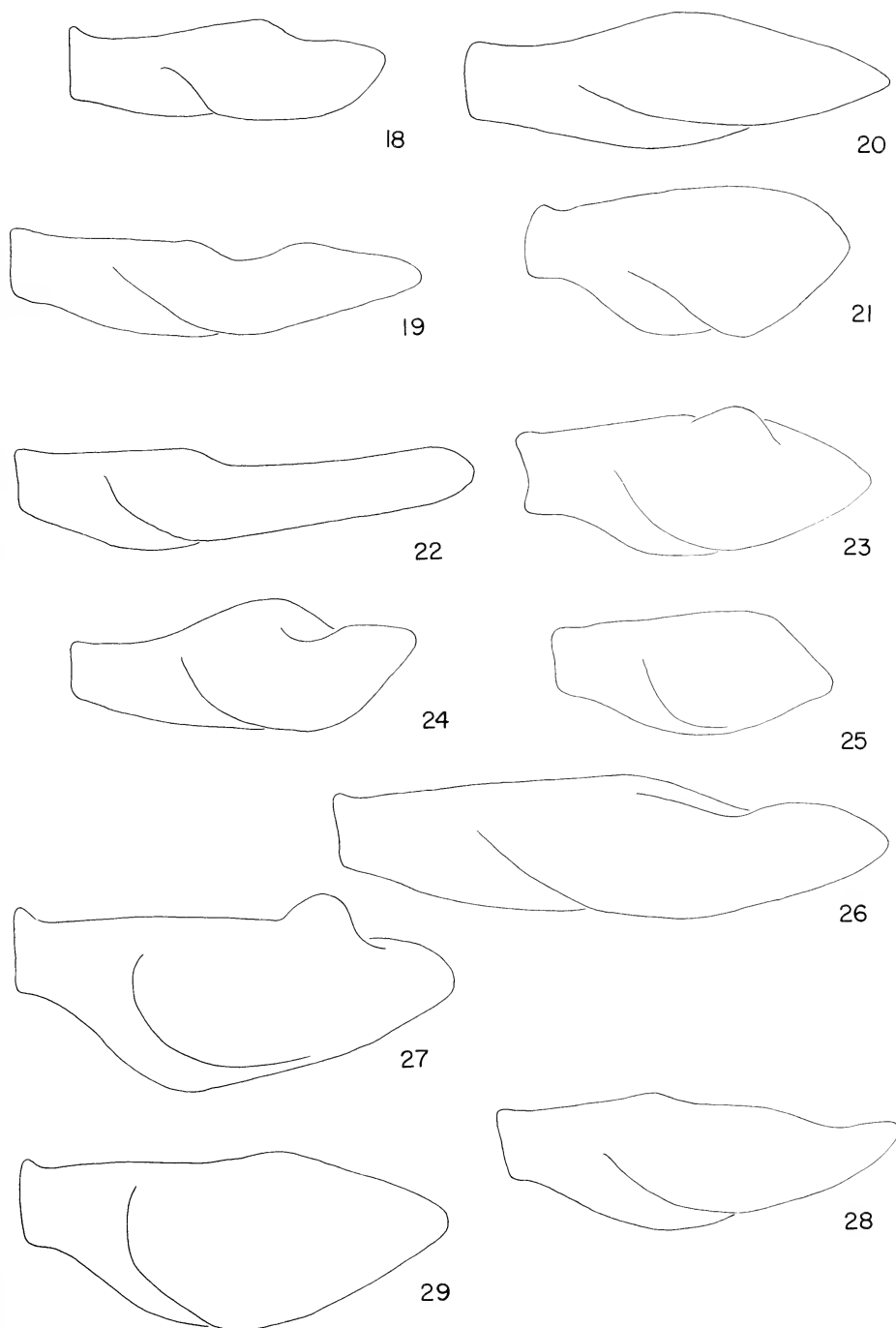
Schizomus portoricensis: Rowland 1973b:197; Rowland and Reddell 1977:79, 80, 87-95; Reddell, 1977:230.

Description (male and female from 1 km S Muna, Yucatán, México).—Male. Color brownish green. Carapace with two pairs of dorsal and two apical setae. Eyespots distinct, vaguely triangular. Anterior sternum with nine bifid setae; posterior sternum with bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata slightly darker than sterna. Flagellum ovoid, with a pair of median depressions. Pedipalpal trochanter produced distally, other segments slightly elongate. Tarsal-basitarsal spurs about 1/7, claw about 1/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 49-6-8-8-8-18. For other leg segment measurements see Rowland and Reddell (1977, Table 1).

Female. Females differ from the males in the following respects: flagellum with three sections; pedipalps not elongate; first legs noticeably shorter; eyespots less distinct; color less greenish. Spermathecae with median and lateral lobes outwardly divergent; medians heavily sclerotized along entire length; laterals much reduced and weakly sclerotized.

Type data.—Of *Stenochrus portoricensis*: holotype female and several paratype females taken at Coamo Springs, Puerto Rico, November 1889 (MCZ, examined); of *Schizomus antilus*: female types taken at Corall [Corral] Nuevo (1500 ft.) and near Havana, Cuba (reportedly deposited in the Pomona College, California, collection, but not located); of *Schizomus cavernicolens*: female holotype taken in Xkyc Cave [=Actún Xkyc], Calcehtok, Yucatán, México, 6 August 1936 (A. S. Pearse) (AMNH, examined); of *Schizomus floridanus*: female holotype taken at Ross and Castellow Hammock, Dade County, Florida, United States (AMNH, examined); of *Schizomus longimanus*: male holotype and female allotype taken in Cueva Cerro Hueco, 3 km SE Tuxtla Gutiérrez, Chiapas, México, 18 August 1967 (J. Reddell, J. Fish, M. Tandy) (AMNH, examined).

Comparisons.—*S. portoricensis* is most similar to and cladistically most proximal to *S. pallidus*. The flagellum is similar in males of the two species, but is longer in *S. pallidus* (0.53 mm) than in *S. portoricensis* (0.42 mm). The females are separable on the basis of



Figs. 18-29.—Lateral views of male flagella of the *mexicanus* group: 18, 19, *S. mexicanus*: 18, from the type locality; 19, from Gómez Farías; 20, *S. lukensi*; 21, *S. bartolo*; 22, *S. reddelli*; 23, *S. moisii*; 24, *S. davisi*; 25, *S. mulaiki*; 26, *S. pallidus*; 27, *S. cookei*; 28, *S. portoricensis* from Cueva Cerro Hueco, Chiapas; 29, *S. mitchelli*.

Table 5.—Measurements (mm) of three species of the *mexicanus* group: 1, one male, *S. moisii*; 2, one female, *S. moisii*; 3, two males, *S. cookei*; 4, three females, *S. cookei*; 5, eight males, *S. mitchelli*; 6, 12 females, *S. mitchelli*. Except as otherwise noted all measurements are of lengths.

	1	2	3	4	5	6
Carapace	1.04	1.13	1.12–1.16	1.17–1.23	1.04–1.16	1.04–1.16
Flagellum						
Length	0.37	0.26	0.43–0.45	0.37–0.38	0.40–0.45	0.28–0.31
Width	0.26	—	0.45–0.45	—	0.35–0.39	—
Leg I						
Femur	1.32	1.11	1.14–1.32	1.09–1.18	1.10–1.24	0.98–1.05
Patella	1.78	1.42	1.37–1.55	1.34–1.39	1.34–1.49	1.12–1.24
Tibia	1.30	1.00	1.03–1.15	1.02–1.07	1.02–1.09	0.87–0.92
Tarsus-Basitarsus	0.95	0.86	0.92–0.97	0.81–0.89	0.87–0.95	0.76–0.81
Leg II						
Femur	0.78	0.70	0.84–0.96	0.79–0.90	0.74–0.82	0.69–0.76
Patella	0.42	0.37	0.45–0.51	0.44–0.50	0.42–0.49	0.39–0.44
Tibia	0.52	0.46	0.59–0.66	0.49–0.59	0.51–0.58	0.41–0.49
Basitarsus	0.50	0.44	0.50–0.52	0.45–0.54	0.48–0.48	0.34–0.43
Leg III						
Femur	0.62	0.67	0.74–0.80	0.76–0.78	0.68–0.74	0.61–0.68
Patella	0.28	0.31	0.30–0.39	0.35–0.39	0.30–0.34	0.29–0.32
Tibia	0.35	0.41	0.41–0.49	0.44–0.48	0.38–0.45	0.31–0.38
Basitarsus	0.40	0.42	0.51–0.57	0.51–0.55	0.45–0.52	0.42–0.45
Leg IV						
Femur	1.18	1.06	1.09–1.24	1.13–1.13	1.04–1.17	0.97–1.05
Patella	0.51	0.43	0.41–0.49	0.46–0.51	0.45–0.50	0.41–0.47
Tibia	0.82	0.80	0.82–0.90	0.84–0.89	0.74–0.83	0.69–0.77
Basitarsus	0.67	0.65	0.71–0.83	0.70–0.76	0.65–0.72	0.59–0.64

the flagellum also, which is longer in *S. pallidus* (0.45 mm) than in *S. portoricensis* (0.30 mm). The carapacial length in both sexes of *S. pallidus* is about 1.4 mm while that of *S. portoricensis* is about 1.25 mm at most, and is usually about 1.05 mm. *S. pallidus* has three pairs of dorsal carapacial setae, whereas *S. portoricensis* has two pairs.

Within its range in México *S. portoricensis* can always be distinguished by its two pairs of dorsal carapacial setae and small size. The only other Mexican species with only two pairs of dorsal setae (*S. pecki* Rowland and *Schizomus* sp., OTU No. 7 from Las Ruinas de Palenque, Chiapas) are large, with a carapacial length in excess of 1.5 mm.

The median spermathecal lobes of this species are heavily sclerotized and are visible without dissection through the genital sternite. No other species in the *mexicanus* group for which females are known possesses so heavy a sclerotization of the median spermathecal lobes.

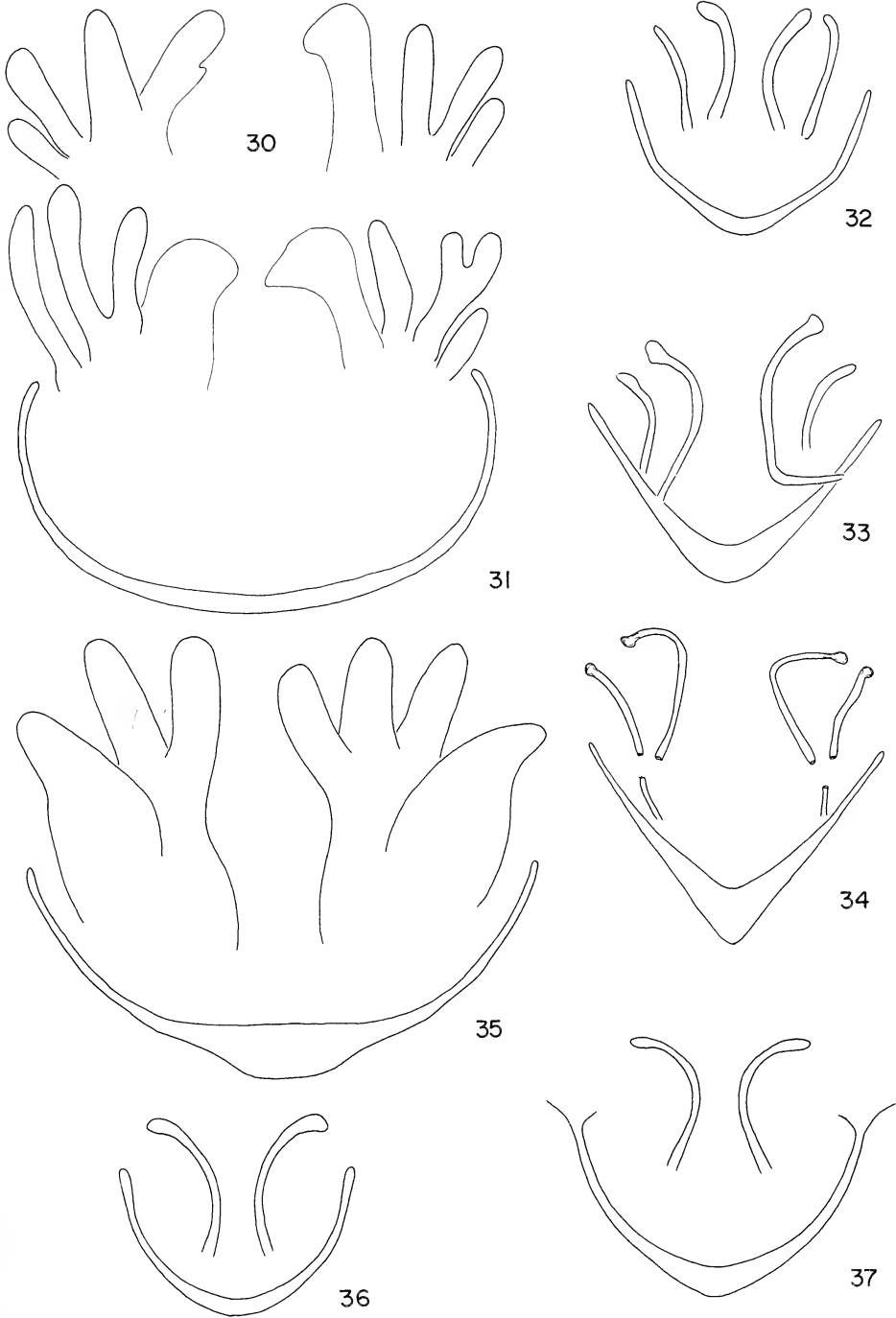
Distribution.—Known from Bermuda, Florida, Campeche, Chiapas, Oaxaca, Veracruz, Yucatán, Quintana Roo, Belize, Guatemala, Nicaragua, Cuba, Dominica, Jamaica, Puerto Rico, Virgin Islands, Colombia, Ecuador, Galapagos Islands, and England (introduced).

Remarks, Variation, and Additional Records.—See Rowland and Reddell (1977).

Schizomus sp., OTU No. 11

Figs. 1, 42

Description.—Female. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Eyespots distinct. Anterior sternum with nine bifid setae. Abdominal



Figs. 30-37.—Female spermathecae of the *mexicanus* group: 30, 31, *S. cookei*; 32-34, *S. mexicanus* from various localities: 32, Nacimiento del Río Frío, Tamaulipas; 33, Cueva Chica, San Luis Potosí; 34, the type locality; 35, *S. mitchelli*; 36, 37, *S. reddelli*: 36, from Cueva de los Vampiros, Tamaulipas; 37, from the type locality.

terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum composed of three sections. Pedipalpal trochanter slightly produced distally; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 28-4-5-5-5-6-14. Other leg segment measurements given in Table 4. Median spermathecae almost horizontally divergent, extremely long, lateral spermathecae short, dome shaped; medians terminate in poorly defined sclerotized bulbs.

Male unknown.

Specimens examined.—Female and immature taken 6 mi. S Valle Nacional, Oaxaca, México (2,000 ft.), 19 May 1971 (S. Peck) (TTU).

Comparisons.—See under *S. moisii*.

Distribution.—Known only from 6 mi. S Valle Nacional, Oaxaca, México.

Schizomus moisii Rowland

Figs. 1, 9, 23, 44

Schizomus moisii Rowland 1973c: 136, 137-139, 140; Rowland and Reddell 1977: 80, 86, 95-96, 99.

Description.—Male. Color brownish green. Carapace with three pairs of dorsal and two apical setae. Eyespots distinct. Anterior sternum with nine bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum diamond shaped, with a pair of median depressions flanked laterally by a pair of swellings. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 44-7-8-7-7-9-16. Other leg segment measurements given in Table 5.

Female. Flagellum composed of three sections. Spermathecae with medians three times longer, but somewhat thinner, than laterals, the latter being dome shaped; medians terminate in a poorly defined sclerotized bulb.

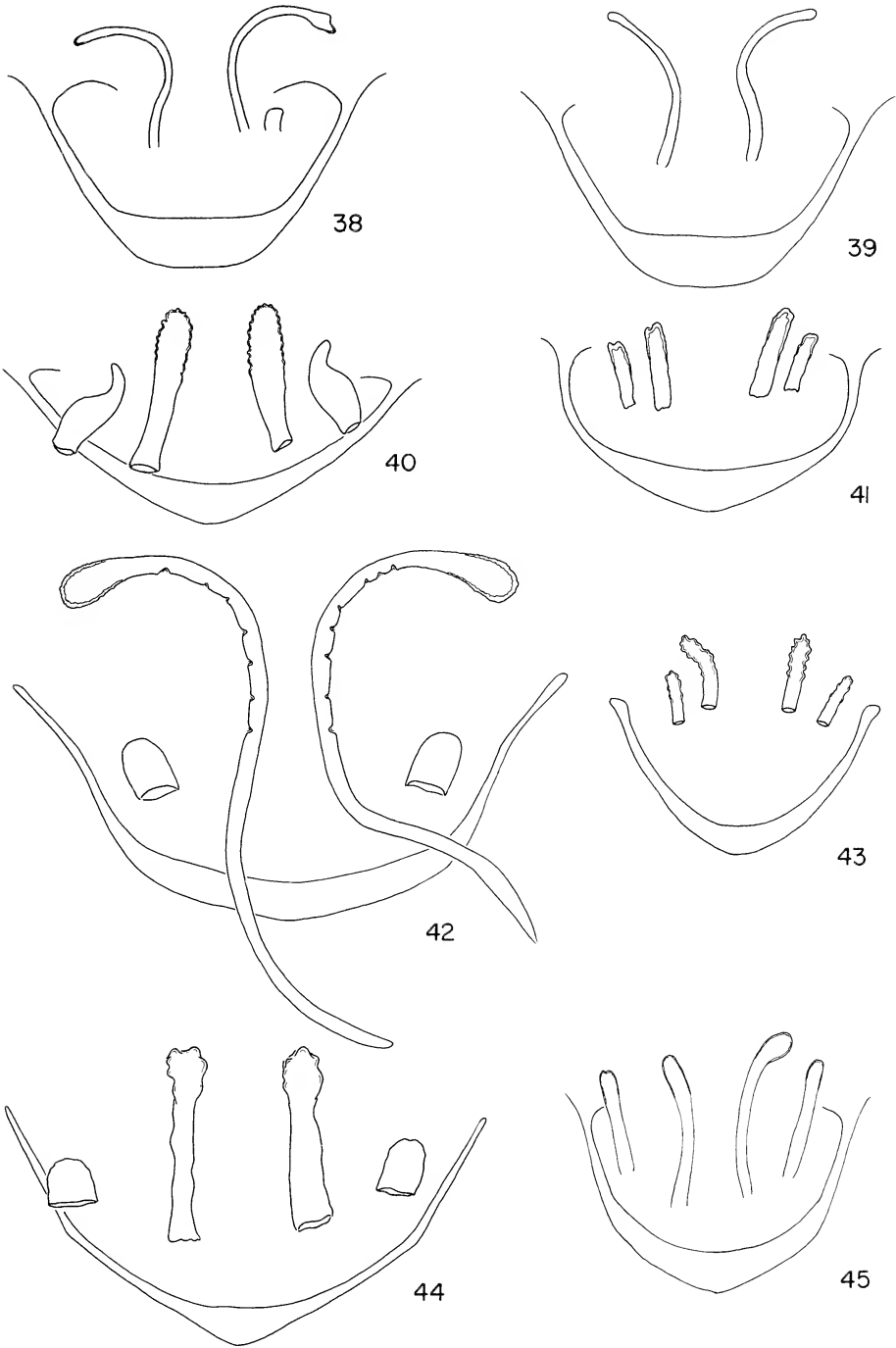
Type data.—Holotype male and allotype female taken in Grutas de Monteflor, 6 km NE Valle Nacional, Oaxaca, México, 28 December 1972 (J. Reddell, D. McKenzie, S. Murphy) (AMNH, examined); five male, five female, and one immature paratypes taken with the holotype (TTU, examined).

Comparisons.—*S. moisii* and its closest relative, OTU No. 11, are distinct from other members of the *mexicanus* group in that they possess a combination of three pairs of dorsal carapacial setae, distinct eyespots, greenish coloration, and short, wide lateral spermathecae. *S. moisii* has straight, short, thick median spermathecae, whereas OTU No. 11 has apically outwardly divergent, very long, and relatively thin medians.

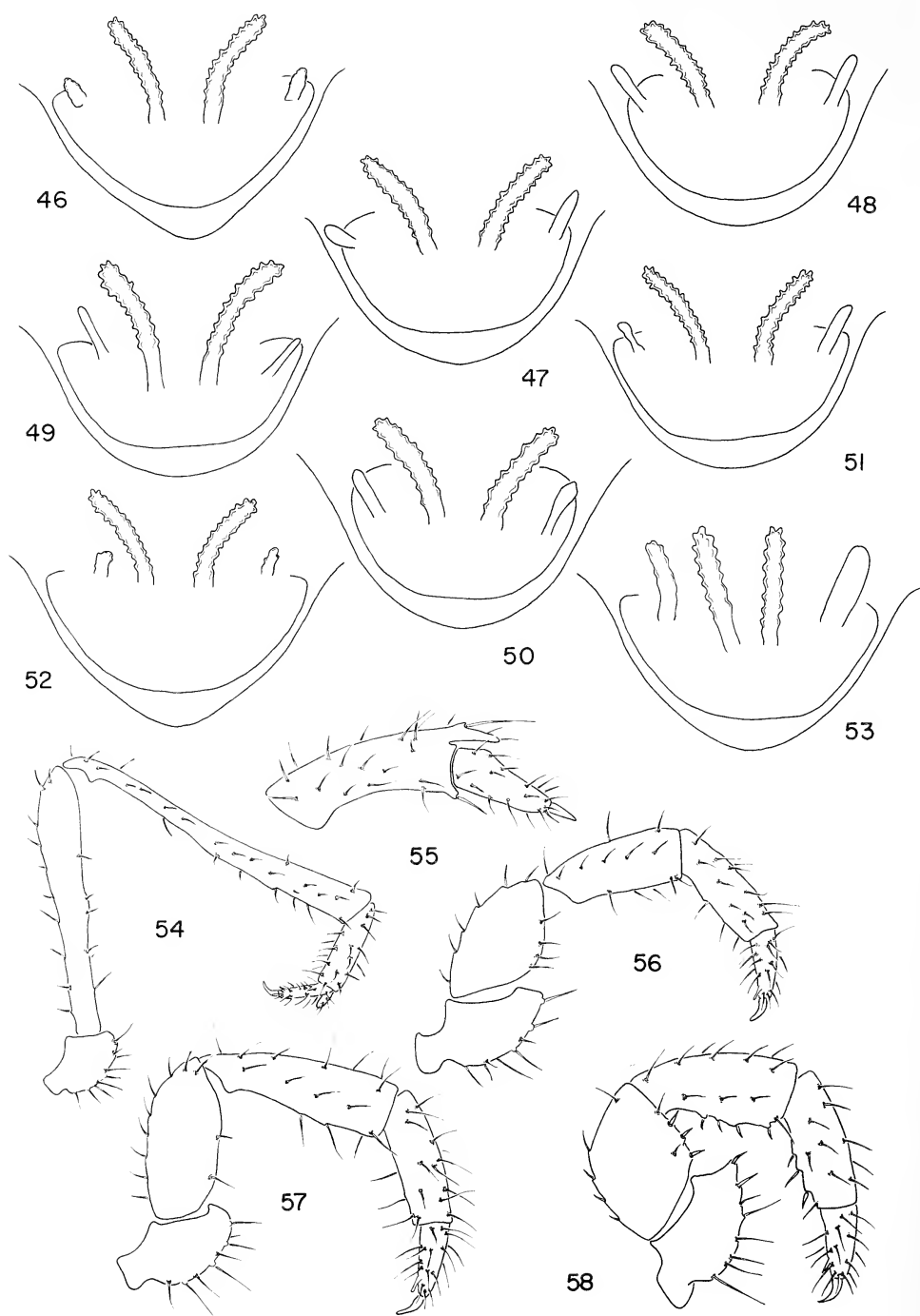
Distribution.—Known only from the type locality.

Remarks.—The dark pigmentation and distinct eyespots indicate that this species is a facultative troglophile and should be found in epigean habitats in the vicinity of the cave. It inhabits Grutas de Monteflor with OTU No. 8, a member of the *pecki* group.

Variation.—The apex of the carapace of the holotype is typical of other schizomids; however, two of the paratypes show variation in this character unlike any we have seen before. These specimens have a truncate margin at the apex of the carapace rather than the typical conical process. There is also only one apical seta rather than the usual two, with the distal seta probably being lost. The significance of this variation is unknown.



Figs. 38-45.—Female spermathecae of the *mexicanus* group: 38, *S. lukensi*; 39, *S. sp. nr. lukensi*, from Cueva de los Cuarteles, Tamaulipas; 40, *S. bartolo*; 41, OTU No. 2; 42, OTU No. 11; 43, *S. pallidus*; 44, *S. moisii*; 45, OTU No. 1.



Figs. 46-58.—Parts of schizomids of the *mexicanus* group: 46-53, female spermathecae of *S. portoricensis* from various localities: 46, the type locality; 47, Cave Bellamar, Cúba; 48, St. Catherine Parish, Jamaica; 49, Dade County, Florida; 50, Guayaquil, Ecuador; 51, Santa Cruz Island, Galapagos Islands; 52, Actún Xkyc, Yucatán; 53, Cueva Cerro Hueco, Chiapas; 54-58, male pedipalps: 54-57, *S. mexicanus* from various localities: 54, right, lateral view from the type locality; 55, dorsal view of tibia and tarsus-basitarsus from the type locality; 56, right, lateral view from Gómez Farías, Tamaulipas; 57, right, lateral view from Sótano del Tigre, San Luis Potosí; 58, right, lateral view of *S. davisi*.

Schizomus cookei Rowland

Figs. 1, 12, 27, 30-31

Schizomus cookei Rowland 1971a:122-123; Reddell and Mitchell 1971a:145; Dumitresco 1973:291; Reddell 1973:38; Rowland 1973c:135; Brignoli 1974:146; Rowland and Reddell 1977:80, 84, 85, 96.

Description.—Male. Color brownish. Carapace with three pairs of dorsal and two apical setae. Eyespots absent. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata very much darker than sterna. Flagellum triangular, with a median pit flanked by lateral swellings. Pedipalpal trochanter produced distally; other segments elongate; the tibia with large spur apposable to tarsus-basitarsus; the latter emarginate with spurs about 1/8, claw about 1/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 35-6-8-7-9-10-22. Other leg segment measurements given in Table 5.

Female. Flagellum composed of three articles. Spermathecae composed of four or five lobes, the medians possibly trifurcate, the terminations not sclerotized, the medians the largest.

Type data.—Holotype male, allotype female, and male and female paratypes taken in El Sótano de la Tinaja, 10 km NNE Ciudad Valles, San Luis Potosí, México, 19 February 1970 (J. A. L. Cooke) (AMNH, examined).

Comparisons.—See under *S. mitchelli*.

Distribution.—This species is known only from two caves north of Ciudad Valles, San Luis Potosí, México.

Remarks.—This troglobitic species occurs sympatrically with *S. mexicanus* and *Agastochizomus lucifer*.

Additional record.—*San Luis Potosí*: Sótano de Yerbaniz, 22.5 km N Ciudad Valles, 8 January 1971 (W. Elliott), one female (TTU, examined).

Schizomus mitchelli Rowland

Figs. 1, 11, 29, 35, 59-62

Schizomus mitchelli Rowland 1971a:121-122; Reddell and Mitchell 1971a:145; Brignoli, 1973:6, Reddell 1973:38; Rowland 1973c:135; Brignoli 1974:145-146; Dumitresco 1977:157; Rowland and Reddell 1977:80, 84, 85, 96.

Description.—Male. Color brownish. Carapace with three pairs of dorsal and two apical setae. Eyespots absent. Anterior sternum with 11 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no evidence of posterodorsal process. Vestigial stigmata very much darker than sterna. Flagellum triangular, with a median pit flanked by slight lateral elevations. Pedipalpal trochanter produced distally; other segments elongate; tibia with spur apposable to tarsus-basitarsus; the latter emarginate with spurs about 1/8, claw about 1/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 35-6-6-7-8-7-19. Other leg segment measurements given in Table 5.

Female. Flagellum composed of three articles. Spermathecae composed of three or four lobes, the medians possibly trifurcate, the terminations not sclerotized, the laterals the largest.

Type data.—Holotype male taken in La Cueva del Pachón, 15 km SSW Ciudad Mante, Tamaulipas, México, 25 November 1967 (S. Fowler and J. Reddell) (AMNH, examined); allotype female and male and female paratypes taken in La Cueva del Pachón, 6 June 1967 (R. Mitchell) (AMNH, examined).

Comparisons.—*S. cookei* is most closely related to *S. mitchelli*. These two species are distinct from other species in the possession of three pairs of dorsal carapacial setae, wide flagella, a single median depression, and strongly dimorphic pedipalps. The distinctive multi-lobed spermathecae serve to distinguish the females of these two species from those of all other species. *S. mitchelli* has no elevations basolateral to the median flagellar pit in the males whereas *S. cookei* has them. The female median spermathecal lobes are narrower than the laterals in *S. mitchelli*, but just the opposite is the case in *S. cookei*.

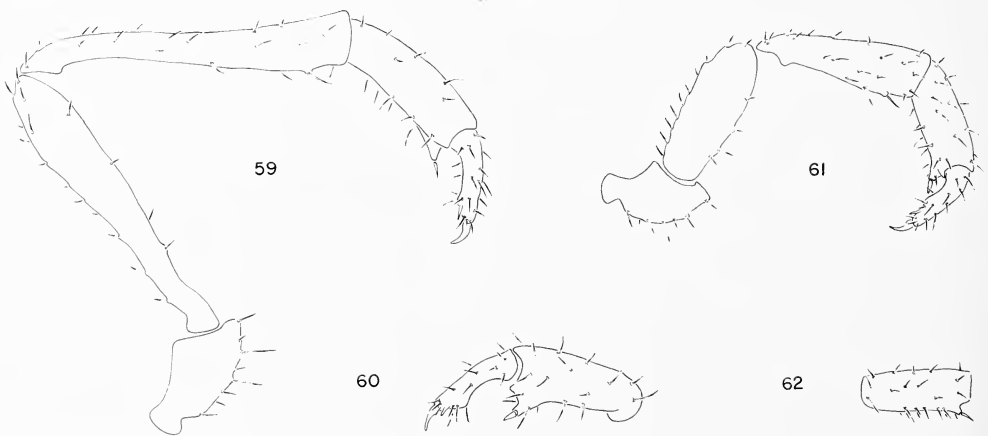
Distribution.—Known only from Cueva del Pachón, Cueva de la Florida, and Grutas de Quintero, Tamaulipas, México.

Remarks.—This species is apparently a troglobite, as is indicated by the lack of eyespots and reduced pigmentation.

Additional records.—See Rowland and Reddell (1977) for other records.

PECKI GROUP

Description.—Members of this group are characterized by large size (1.33-1.76 mm carapacial length). The color is brownish. Eyespots vary from absent to indistinct to distinct. Suspected troglobites lack eyespots. The carapace has two or three pairs of dorsal and two apical setae; the median pair of the dorsal setae of those species with three pairs is invariably the smallest. Males: abdomen never attenuated; posterodorsal process absent; flagella large and bulbous. Females: spermathecae characterized by the median pair usually being much longer than the lateral pair; laterals are absent in some species, but in others are nearly as long as the medians; without much terminal enlargement or



Figs. 59-62.—Male pedipalps of *S. mitchelli*: 59, right, lateral view; 60, right, mesal view of tibia and tarsus-basitarsus only; 61, right, lateral view; 62, left, dorsal view.

localized sclerotization. The pedipalps are very stout in both sexes and do not exhibit dimorphism. The pedipalpal claws are large, usually $2/3$ and up to $3/4$ the length of the tarsus-basitarsus.

Distribution.—México: Veracruz, Oaxaca, Tabasco, Chiapas. Belize. Guatemala.

Remarks.—See Table 6 for comparisons of the species in the *pecki* group.

Subordinate taxa.—OTU No. 8; *firstmani* complex: *S. firstmani*, OTU No. 2, *S. sp. cf. sbordonii*; *pecki* complex: *S. pecki*, *S. guatemalensis*, OTU No. 6, OTU No. 7.

Schizomus sp., OTU No. 8

Figs. 63, 81

Schizomus sp. 5: Rowland and Reddell 1977:80, 86, 96, 99.

Description.—Female. Color brownish. Carapace with three pairs of dorsal, the medians very small, and two apical setae. Eyespots distinct. Anterior sternum with nine bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum composed of four articles, not distally expanded, elongate. Pedipalpal trochanter produced slightly distally; tarsal-basitarsal spurs about $1/4$, claw about $2/3$ length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 41-7-8-9-10-10-18. Other leg segment measurements given in Table 7. Median and lateral spermathecae slightly convergent, medians about twice as long as laterals, both slightly more sclerotized apically than basally, medians terminating in vague bulbs.

Male unknown.

Type data.—Female and immature taken in Grutas de Monteflor, 6 km N Valle Nacional, Oaxaca, México, 28 December 1972 (J. Reddell, D. McKenzie, M. McKenzie, S. Murphy) (TTU).

Comparisons.—This taxon is unique among members of the *pecki* group in that the female flagellum is not at all expanded distally. In those species possessing three pairs of dorsal carapacial setae, OTU No. 8 is the only one in which the spermathecal tips are sclerotized.

Distribution.—Known only from Grutas de Monteflor, Oaxaca, México.

Remarks.—This species inhabits Grutas de Monteflor with *S. moisii*, a facultative troglophile. The distinct eyespots and moderate pigmentation of OTU No. 8 are also indicative that it is a facultative troglophile.

Schizomus firstmani Rowland

Figs. 63, 65, 67-68, 74-75

Schizomus sp.: Reddell 1971a:219 [Grutas de Atoyac record only].

Schizomus firstmani Rowland 1973a:7, 15, 16-19; Rowland 1973c:136; Dumitresco 1977:157; Rowland and Reddell 1977:80, 84, 98.

Description.—Male. Color brownish. Carapace with three pairs of dorsal, medians very small, and two apical setae. Eyespots absent. Anterior sternum with eight bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII with no

Table 6.—Comparisons of members of the *pecki* group. See the introduction to Rowland and Reddell (1979a) for discussion of characters.

CHARACTER	first- mani	OTU #2	sbor- donii	pecki	guatem- alensis	OTU #6	OTU #7	OTU #8
DORSAL SETAE	3	3	3	2	2	2	2	3
STERNAL SETAE	8	9	9	8	10	13	9	9
EYESPOTS	absent	indis- tinct	distinct	indis- tinct	indis- tinct	absent	indis- tinct	distinct
SPERMA- THECAE	laterals absent	M 2X L	M 3X L	M 2X L	M 4X L	M \pm L	M \pm L	M 2X L
CARAPACAL LENGTH	1.40	1.54	1.52	1.58	1.33	1.41	1.76	1.49
DISTAL EXP. FEM. FLAG.	strong	strong	slight	slight	?	slight	none	none
LENGTH FEM. FLAGELLUM	.38	.47	.39	.46	?	.41	.47	.45
PIT MALE FLAGELLUM	absent	?	?	single	?	?	?	?

evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum compressed laterally, expanded distally, with complex sculpturing. Pedipalpal trochanter produced slightly distally; tarsal-basitarsal spurs about 1/3, claw about 2/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 53-8-10-10-10-13-24. Other leg segment measurements given in Table 7.

Female. Flagellum composed of three articles, expanded greatly distally. Median spermathecae only present, long slender, slightly divergent apically, terminating in slight bulbs.

Type data.—Holotype male and immature paratype taken in Grutas de Atoyac, 2 km E Atoyac, Veracruz, México, 24 December 1971 (D. McKenzie) (AMNH, examined); allotype female taken in Grutas de Atoyac, 6 August 1969 (S. and J. Peck) (AMNH, examined); female and three immature paratypes taken in Grutas de Atoyac, 22 August 1965 (J. Reddell, J. Fish, W. Bell) (AMNH, examined).

Comparisons.—This species appears to be most closely related to OTU No. 2. Both species have the female flagellum greatly enlarged distally. This character serves to distinguish them from other American species. *S. firstmani* lacks the lateral spermathecae, whereas OTU No. 2 has them. OTU No. 2 also has a much longer flagellum (0.47 mm) than *S. firstmani* (0.38 mm).

Distribution.—This species is known with certainty only from the type locality; females from three caves in northern Oaxaca are tentatively identified as *S. firstmani*.

Remarks.—This species appears to be a troglobite. It inhabits Grutas de Atoyac with a troglophile species (*Schizomus* sp. cf. *sbordonii*). Females from the three Oaxacan caves (about 30 km distant) are indistinguishable from females of *S. firstmani* and are placed here pending discovery of males. It is, however, doubtful if genetic interchange is possible between these two areas and it is probable that they are recently isolated species of a once wider ranging epigeal population.

Additional records.—*Oaxaca*: Cueva Desapareciendo, 2 km W Acatlán, 5 January 1976 (A. Grubbs), 1 female (TTU); Cueva de la Finca, 10 km SW Acatlán, 31 December 1976 (J. Reddell, A. Grubbs, D. McKenzie), 1 female (TTU); Cueva del Nacimiento del Río San Antonio, 10 km S Acatlán, 26 December 1972 (J. Reddell, D. McKenzie, M. McKenzie, S. Murphy), 1 female, 3 immatures (TTU); Veracruz: Grutas de Atoyac, 6 January 1977 (J. Reddell), 2 females, 1 immature (TTU).

Schizomus sp., OTU No. 2
Figs. 63, 70-71, 77, 82

Schizomus sp. 3: Rowland and Reddell 1977:80, 86, 99.

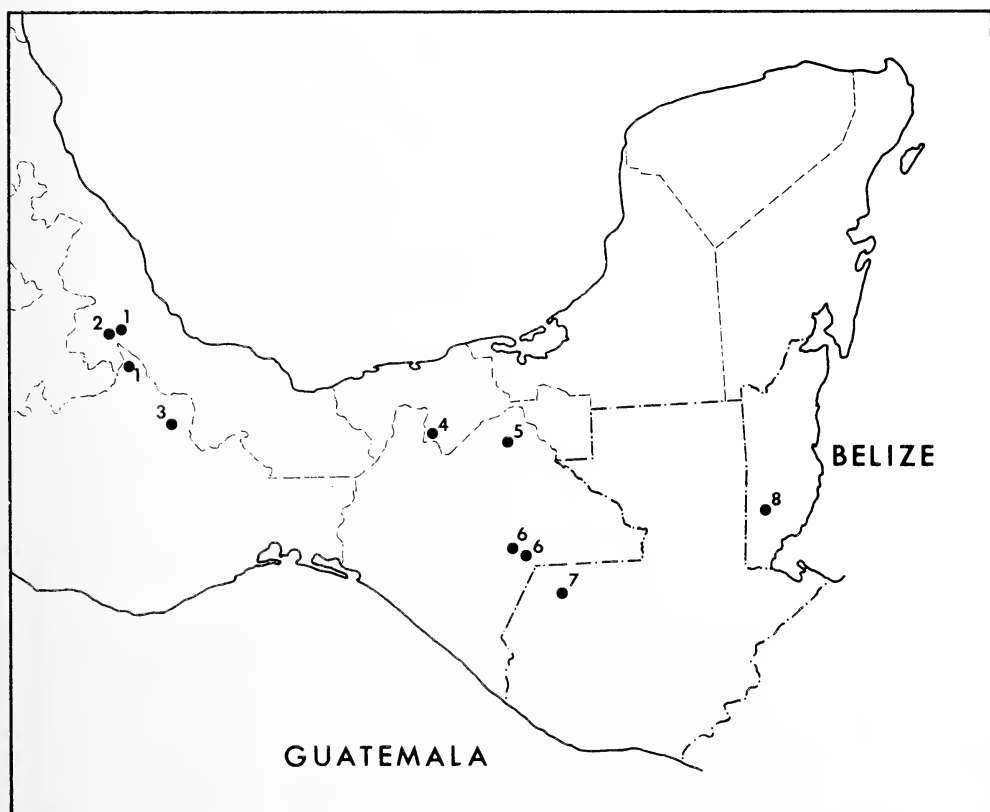
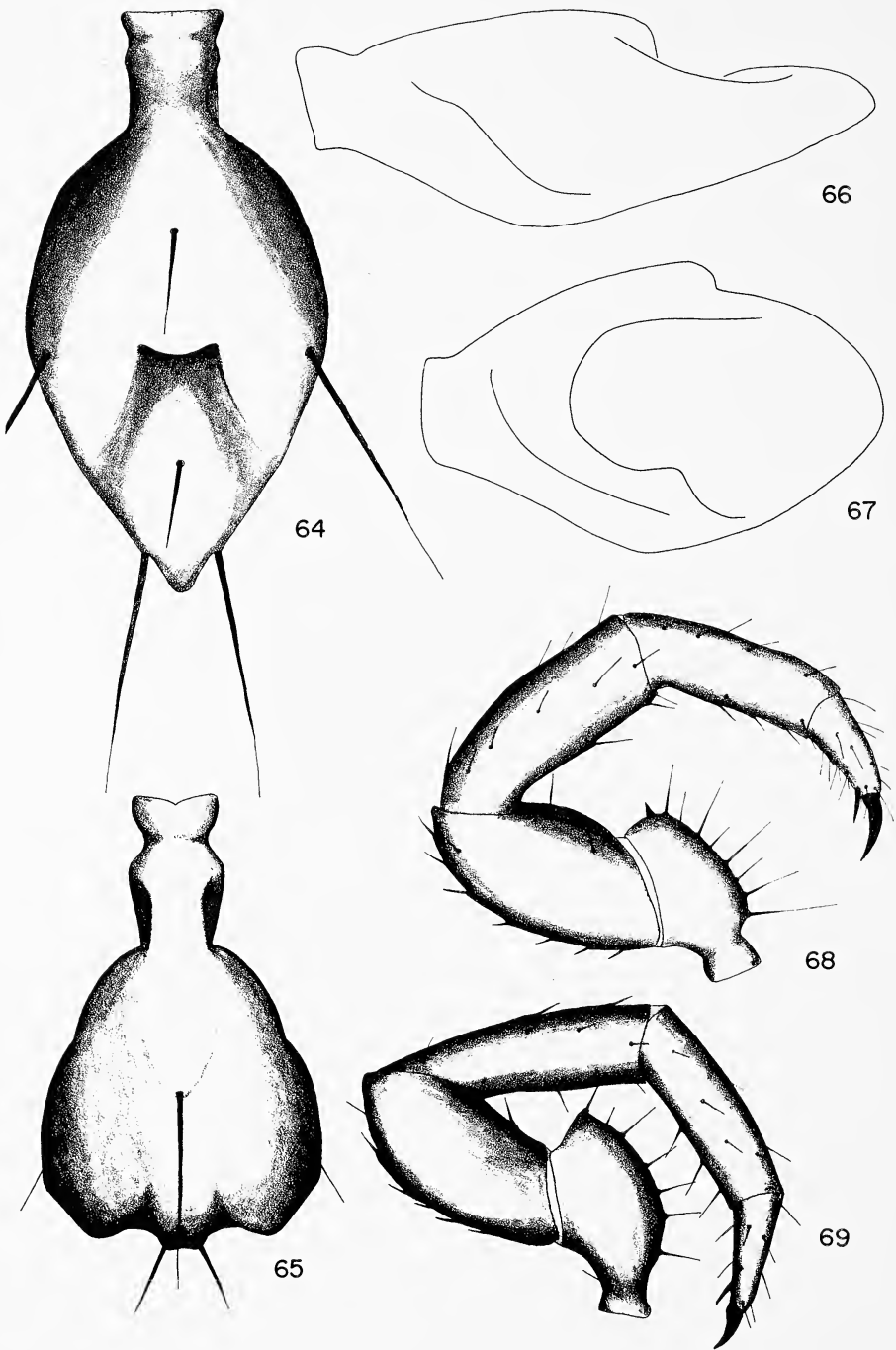


Fig. 63.—Map showing distribution of schizomids of the *pecki* group: 1, *S. firstmani*; 2, *S. sp. cf. sbordonii*; 3, OTU No. 8; 4, *S. pecki*; 5, OTU No. 7; 6, OTU No. 2; 7, *S. guatemalensis*; 8, OTU No. 6.



Figs. 64-69.—Parts of schizomids of the *pecki* group: 64-67, male flagella: 64, 65, dorsal views: 64, *S. pecki*; 65, *S. firstmani*; 66, 67, lateral views: 66, *S. pecki*; 67, *S. firstmani*; 68, 69, lateral views of right pedipalps: 68, *S. firstmani*; 69, *S. pecki*.

Description.—Female. Color brownish. Carapace with three pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with nine bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum composed of three articles, markedly expanded distally. Pedipalpal trochanter greatly produced distally; tarsal-basitarsal spurs about 1/4, claw about 2/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 51-8-10-8-11-10-21. Other leg segment measurements given in Table 7. Median spermathecae twice length of laterals, both divergent, medians curved, with slight bulbs, but no special sclerotization.

Male unknown.

Specimens examined.—Female taken in Grutas de Zapaluta, 4 mi. SE Zapaluta, Chiapas, México, 19 July 1950 (C. and M. Goodnight) (AMNH); female taken in Grutas de Zapaluta, 20 August 1967 (J. Reddell, J. Fish, T. Evans) (TTU); three females and six immatures taken in Grutas de Zapaluta, 28 August 1972 (R. Mitchell, J. Cooke) (TTU); one female and one immature, taken in Sumidero del Camino, 10 mi. NE Comitán, Chiapas, 22 August 1967 (J. Reddell, J. Fish) (TTU); one immature taken in Cueva Chica de Hun Chabín, near Comitán, Chiapas, 21 August 1967 (J. Reddell) (TTU).

Comparisons.—See under *S. firstmani*.

Distribution.—Known only from three caves near Comitán, Chiapas, México.

Remarks.—This species is known only from caves, but does not show the advanced troglotic facies of *S. firstmani*. It is probably a facultative troglophile.

Schizomus sp., cf. *sbordonii* Brignoli

Figs. 63, 73

Schizomus sbordonii Brignoli 1973:7, 8, 9; Rowland 1973c:135, 136; Brignoli 1974:146, 147, 149; Rowland and Reddell 1977:80, 86, 98.

Description (female from Cueva de Atoyac)—Color brownish. Carapace with three pairs of dorsal and two apical setae. Eyespots distinctly round. Anterior sternum with nine bifid setae. Abdominal terga I-V, VII with two setae, terga VI with three setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum long, composed of three articles, slightly expanded distally. Pedipalpal trochanter produced distally, tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 48-8-9-10-11-23. Other leg segment measurements given in Table 7. Median spermathecae three times longer than laterals, both divergent, medians with apical half sclerotized, medians and laterals without terminal bulbs.

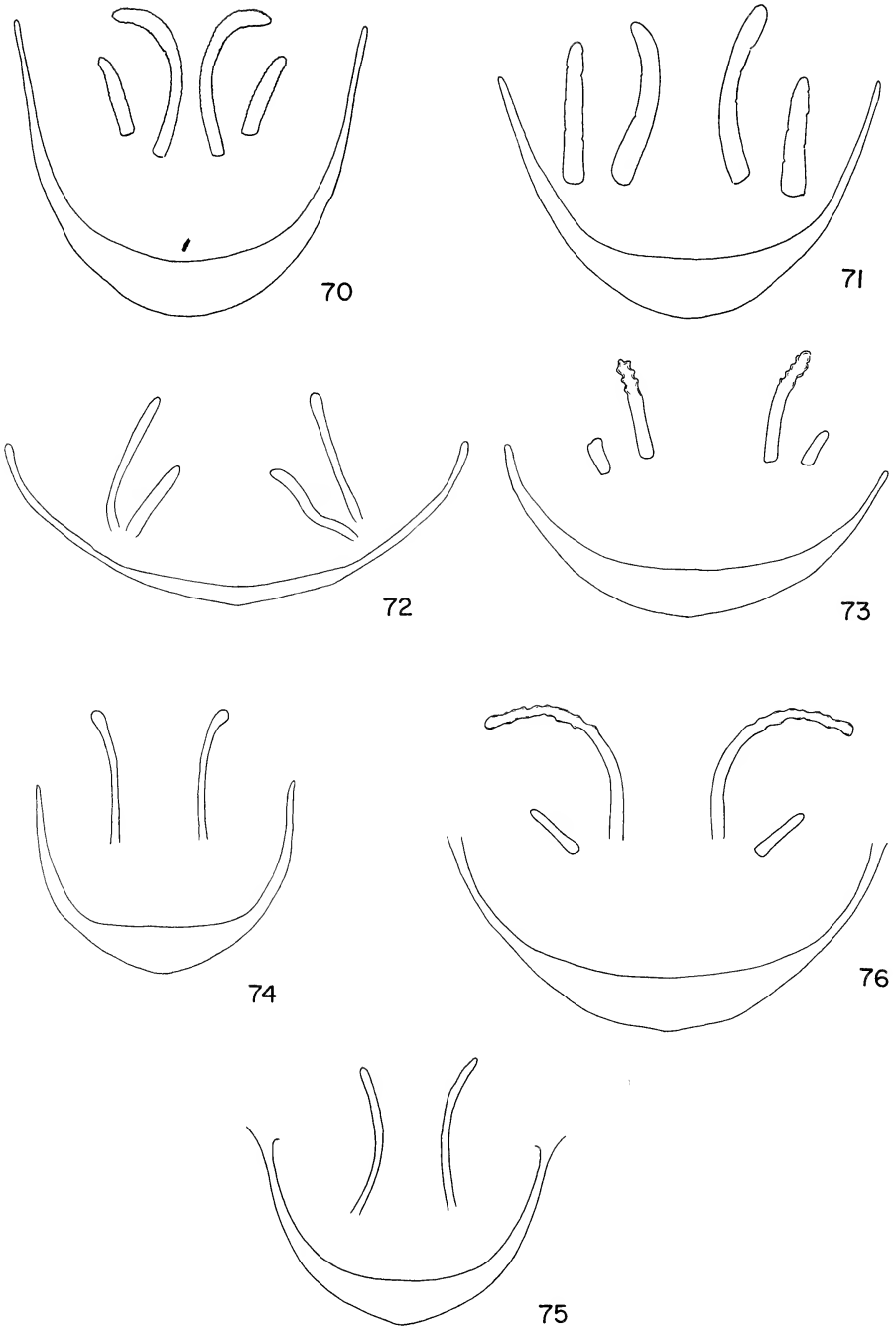
Male unknown.

Type data.—Female holotype taken in Cueva de Ojo de Agua Grande, near Córdoba, Veracruz, México, 5 November 1969 (V. Sbordonii) (IZR, not examined).

Specimen examined.—Female taken in Cueva de Atoyac, 2 km E Atoyac, Veracruz, México, 6 August 1969 (S. and J. Peck) (TTU).

Comparisons.—The specimen studied is very similar to *S. firstmani* and OTU No. 2 in most respects, but differs from them in having very distinct and round eyespots, only a slight expansion of the flagellum, darker pigmentation, and three setae on terga VI.

Distribution.—*S. sbordonii* is known with certainty only from the type locality; the specimen examined is from a cave in the same mountain range.



Figs. 70-76.—Female spermathecae of the *pecki* group: 70, 71, OTU No. 2: 70, from Grutas de Zapaluta, Chiapas; 71, from Sumidero del Camino, Chiapas; 72, OTU No. 7; 73, *S. sp. cf. sbordonii*; 74, 75, *S. firstmani*: 74, from the type locality; 75, from Cueva del Nacimiento del Río San Antonio, Oaxaca; 76, *S. guatemalensis*.

Table 7.—Measurements (mm) of species of the *pecki* group: 1, one male, *S. firstmani*; 2, one female, *S. firstmani*; 3, three females, OTU No. 2; 4, one female, *S. sp. cf. sbordonii*; 5, one male, *S. pecki*; 6, two females, *S. pecki*; 7, one female, *S. guatemalensis*; 8, one female, OTU No. 6; 9, one female, OTU No. 7; 10, one female, OTU No. 8. Unless other noted all measurements are of lengths.

	1	2	3	4	5	6	7	8	9	10
Carapace	1.25	1.40	1.46–1.54	1.52	1.31	1.55–1.58	1.33	1.41	1.76	1.49
Flagellum										
Length	0.46	0.38	0.46–0.47	0.37	0.60	0.46–0.47	—	0.41	0.47	0.45
Width	0.29	—	—	—	0.29	—	—	—	—	—
Leg I										
Femur	1.85	1.78	1.81–1.87	1.67	2.24	2.05–2.44	1.32	1.53	2.04	1.57
Patella	2.12	2.13	2.08–2.18	2.20	3.74	2.50–2.51	1.56	1.90	2.50	1.90
Tibia	1.48	1.45	1.46–1.50	1.69	2.12	1.88–1.94	1.12	1.44	1.85	1.41
Tarsus-Basitarsus	1.20	1.20	1.20–1.24	1.19	1.25	1.15–1.16	0.99	1.13	1.20	1.03
Leg II										
Femur	1.15	1.18	1.28–1.35	1.22	1.21	1.20–1.36	0.98	1.06	1.45	1.09
Patella	0.56	0.62	0.65–0.73	0.68	0.57	0.61–0.70	0.51	0.54	0.77	0.62
Tibia	0.80	0.80	0.86–0.94	0.84	0.90	0.85–0.85	0.61	0.71	1.00	0.72
Basitarsus	0.59	0.63	0.72–0.76	0.67	0.79	0.73–0.77	0.54	0.55	0.75	0.57
Leg III										
Femur	1.00	1.07	1.20–1.23	1.07	1.10	1.17–1.20	0.87	0.93	1.22	0.95
Patella	0.40	0.52	0.56–0.64	0.55	0.50	0.55–0.59	0.43	0.44	0.58	0.45
Tibia	0.69	0.67	0.80–0.84	0.72	0.75	0.71–0.74	0.50	0.55	0.75	0.54
Basitarsus	0.63	0.73	0.78–0.86	0.73	0.80	0.83–0.84	0.61	0.63	0.82	0.62
Leg IV										
Femur	1.63	1.65	1.78–1.86	1.04	1.96	1.82–1.93	1.34	1.48	1.90	1.49
Patella	0.62	0.68	0.76–0.79	0.75	0.65	0.63–0.83	0.62	0.62	0.80	0.67
Tibia	1.18	1.12	1.28–1.31	1.20	1.36	1.30–1.37	0.92	1.02	1.38	1.08
Basitarsus	1.02	1.04	1.15–1.19	1.01	1.14	1.04–1.11	0.85	0.89	1.16	0.91

Remarks.—The specimen described from Cueva de Atoyac is considered likely to be identical to *S. sbordonii* on geographical grounds. The description and illustrations given by Brignoli (1973, 1974), while inadequate to recognize any species, do not contraindicate the specimen studied. The types of *S. firstmani* were collected with the specimen tentatively assigned to *S. sbordonii*. Recent collections of the inner chambers of Cueva de Atoyac have included only *S. firstmani*; *S. sp. cf. sbordonii* may have been found near the entrance. *S. sbordonii* is probably a facultative troglophile.

Schizomus pecki Rowland
Figs. 63-64, 66, 69, 79

Schizomus pecki Rowland 1973a:7, 16, 19-23; Rowland 1973c:136; Sbordonii, Agrano, and Zullini 1974:14-15; Dumitresco 1977:157; Rowland and Reddell 1977:80, 83, 84, 98-99.

Description.—Male. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with eight entire setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae, segment XII without evidence of posterodorsal process. Vestigial stigmata darker than sterna. Flagellum lanceolate, with a

median depression following a single median gentle elevation. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/5, claw about 2/3 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 62-8-10-9-9-19. Other leg segment measurements given in Table 7.

Female. Flagellum composed of three articles, slightly expanded distally. Median spermathecae twice length of laterals, both divergent, medians curved, but without terminal bulbs, both pair with light sclerotization along distal half of both lobes.

Type data.—Holotype male taken in Las Grutas del Coconá, 2 mi. NE Teapa, Tabasco, México, 1 August 1948 (C. Goodnight) (AMNH, examined); allotype female and paratype female taken in Las Grutas del Coconá, 29 November 1971 (D. McKenzie) (AMNH, examined).

Comparisons.—The presence of two pairs of dorsal carapacial setae serves to distinguish *S. pecki* from *S. firstmani*, *S. sp. cf. sbordonii*, and OTU No. 2. This species is also distinct in possessing a long (0.40 mm), slightly expanded flagellum. The pedipalpal claw of *S. pecki* is distinctly smaller than that of OTU No. 7 and distinctly larger than that of OTU No. 6 and *S. guatemalensis*. The medians of the spermathecae of *S. pecki* are shorter than are those of *S. guatemalensis*, but are longer than are those of OTU No. 6 and OTU No. 7.

Distribution.—Known only from two caves 3 km NE Teapa, Tabasco, México.

Remarks.—*S. pecki* is apparently a troglobite. It has been found in abundance on silt under rotten wood in the more remote sections of Grutas del Coconá. The troglophilic *S. trilobatus* Rowland inhabits leaf litter near the entrance of the cave.

Additional records.—*Tabasco*: Grutas del Coconá, 24 July 1973 (J. Reddell, J. M. Rowland), 3 females, 3 immatures (TTU); Resumidero del Coconá, 3 km NE Teapa, 14 June 1975 (J. Reddell, A. Grubbs), 1 immature (TTU).

Schizomus guatemalensis Chamberlin

Figs. 63, 76

Schizomus guatemalensis Chamberlin 1922:12; Mello-Leitão 1931:17; Giltay 1935:6; Gertsch 1941:14; Takashima 1943:93; Rowland and Reddell 1977:99.

Description.—Female. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with 10 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum missing. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/5, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 40-6-8-7-9-9-20. Other leg segment measurements given in Table 7. Median spermathecae long and slender, strongly curved outwardly, lightly sclerotized along distal 2/3, terminating in a slight bulb; laterals about 1/4 as long, straight, but directed diagonally outward, no terminal bulb or special sclerotization.

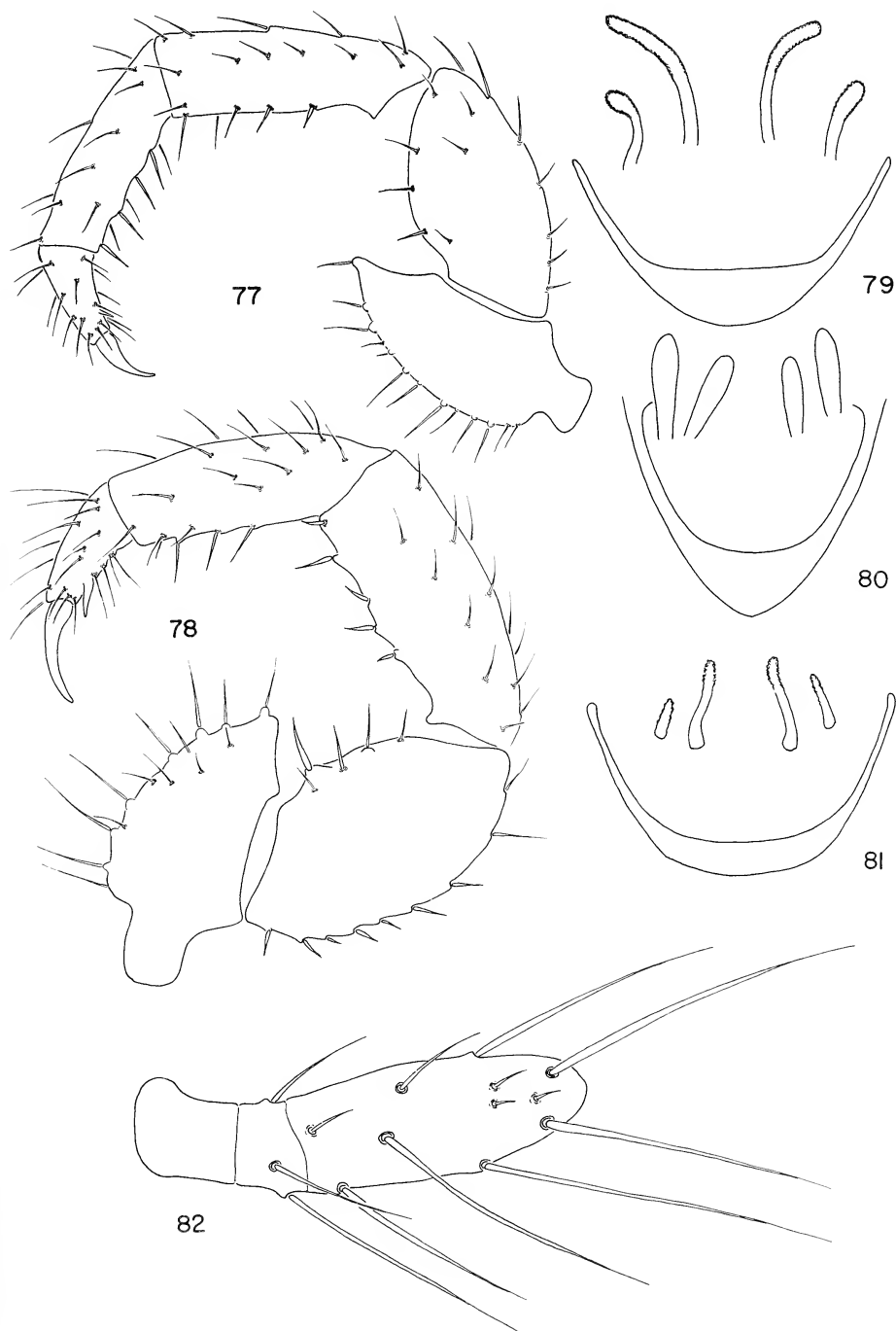
Male unknown.

Type data.—Holotype female taken at San Rafael, Guatemala (MCZ, examined).

Comparisons.—See under *S. pecki*.

Distribution.—Known only from the type locality.

Remarks.—The type locality cannot be identified with certainty to any of the several communities of the name San Rafael in Guatemala.



Figs. 77-82.—Parts of schizomids of the *pecki* group: 77, 78, lateral views of female left pedipalps: 77, OTU No. 2; 78, OTU No. 7; 79-81, spermathecae: 79, *S. pecki*; 80, OTU No. 6; 81, OTU No. 8; 82, lateral view of flagellum of OTU No. 2.

Schizomus sp., OTU No. 6

Figs. 63, 80

Schizomus sp. 4: Rowland and Reddell 1977:80.

Description.—Female. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots absent. Anterior sternum with 13 bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum composed of three articles, long, slightly distally expanded. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/4, claw about 1/2 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 45-8-9-10-11-20. Other leg segment measurements given in Table 7. Median and lateral spermathecae about same size, slightly convergent, gradually expanded distally; no special sclerotization or apical bulbs.

Male unknown.

Specimen examined.—Female taken in St. Herman's Cave (400 ft.), Caves Branch, British Honduras [=Belize], between 23 July and 21 August 1972 (S. and J. Peck) (AMNH).

Comparisons.—See under *S. pecki*.

Distribution.—Known only from St. Herman's Cave, Belize.

Remarks.—The very light pigmentation and lack of eyespots in this species suggests that it is an obligate cavernicole.

Schizomus sp., OTU No. 7

Figs. 63, 72, 78

Description.—Female. Color brownish. Carapace with two pairs of dorsal and two apical setae. Eyespots indistinct. Anterior sternum with nine bifid setae. Abdominal terga I-VII with two setae, terga VIII-IX with four setae. Vestigial stigmata darker than sterna. Flagellum broken, but appearing not to be greatly expanded distally. Pedipalpal trochanter produced distally; tarsal-basitarsal spurs about 1/3, claw about 3/4 length of tarsus-basitarsus. Tarsal-basitarsal segments of leg I of the following approximate proportions: 50-7-10-9-9-11-24. Other leg segment measurements given in Table 7. Median spermathecae slightly smaller than laterals, both convergent, not sclerotized, not terminating in bulbs.

Male unknown.

Specimens examined.—Female taken at Las Ruinas de Palenque, Chiapas, México, July 1948 (C. and M. Goodnight) (AMNH); two immatures taken at Las Ruinas de Palenque, 25 July 1973 (J. Reddell) (TTU).

Comparisons.—This species seems to be most closely related to *S. pecki* in that they share a similarity in development of the spermathecae, and two pairs of dorsal carapacial setae. The pedipalpal claw is relatively shorter in *S. pecki* than in OTU No. 7; the carapace of *S. pecki* is also shorter (1.55-1.58 mm) than is that of OTU No. 7 (1.76 mm). See also under *S. pecki*.

Distribution.—Known only from Las Ruinas de Palenque, Chiapas, México.

Remarks.—This species was found under rocks on the deeply shaded canyon walls above the ruins.

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REVISION OF THE GENUS *NEBO* SIMON (SCORPIONES: DIPLOCENTRIDAE)

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ABSTRACT

A taxonomic revision of the genus *Nebo* Simon, based largely on adult morphometric characters is presented. *Nebo hierichonticus* (Simon) and *Nebo flavipes* Simon are recognized as valid species: *Nebo hierichonticus pallidimanus* Pocock is a junior synonym of *N. flavipes*; *Nebo grandis*, n. sp., *Nebo henjamicus*, n. sp., *Nebo omanensis*, n. sp. and *Nebo yemenensis*, n. sp. are described.

INTRODUCTION

The family Diplocentridae Karsch contains two subfamilies: Diplocentrinae Kraepelin with six genera found almost exclusively in the New World, and Nebinae Kraepelin with the genus *Nebo* Simon from the Middle East and the Arabian Peninsula (Francke 1977a, 1978b).

Four nominal taxa have been assigned to *Nebo* in the past: *Hemiscorpio hierichonticus* Simon, type species of the genus, from Egypt, Israel and Jordania is a fairly well known species; *Nebo hierichonticus pallidimanus* Pocock, from Yemen has received little attention since its description; *Nebo flavipes* Simon, also from Yemen and regarded by many previous authors as a junior synonym of *N. hierichonticus*; and finally, *Diplocentrus sulcatus* Karsch, from "Africa", long regarded a junior synonym of *N. hierichonticus*. The type specimens of *D. sulcatus* could not be located for this study and are presumably lost or destroyed; this taxon is listed as a junior synonym of *N. hierichonticus* following earlier authors. The type specimens of *N. hierichonticus pallidimanus* apparently were never labelled as such; however, two specimens mentioned in the original description were studied and one has been designated lectotype. The type specimens of *N. hierichonticus* and *N. flavipes* were studied by Vachon (1965), who noted some differences between them, and made the following remarks:

"Il est donc probable, dans le cadre de l'espèce *hierochonticus*, que d'importantes variations relatives à la taille, à la coloration, aux indices morphométriques peuvent être mises en évidence; seule l'étude de populations (et surtout la comparaison de spécimens de même âge) habitant diverses stations allant de la Syrie à l'Arabie orientale, apportera la solution d'un problème de taxonomie qui, dès maintenant, nous paraît être complexe."

This study is based on the examination of about 100 specimens of *Nebo* available to me, and attempts to provide a solution to the complex taxonomic problem alluded to by Vachon.

METHODS

The genus *Nebo* is very homogeneous in the overall external appearance of its members. Characters that have been successfully used in taxonomic studies of members of the subfamily Diplocentrinae (Francke 1977a, 1977b, 1977c, 1978a, 1978b) proved taxonomically worthless for *Nebo*. Meristic characters, such as pectinal tooth counts and tarsomere II spine counts, show as much, or more, intrapopulation variation as interpopulation variation. Direct comparisons of specimens, however, indicated conspicuous as well as subtle morphometric differences between specimens from various localities. Therefore, a morphometric analysis such as that of Francke (1975) was undertaken.

Initially 20 morphometric ratios based on 24 measurable characters (measured at 10X) were calculated for each specimen. Analyses of these ratios for 45 *N. hierichonticus* from Israel revealed considerable allometry and moderate to extensive sexual dimorphism. The lack of adequate samples from other parts of the range of *Nebo*, and a recurring inability to accurately determine stadia in scorpions forced me to eliminate all but mature specimens from further analyses. Sexual maturity in males was established by the presence of fully developed paraxial organs, and was found to be perfectly correlated with the presence of prominent scallops on the pedipalp chela fingers. Females lack scallops on the pedipalp chela fingers, and sexual maturity was established by examination of the reproductive system in some cases, or was assumed on the basis of size. Considerable allometry was detected between adult and subadult males, whereas there appeared to be little or none between adult and subadult females, making accurate aging less critical. The results presented herein, therefore, apply only to adults in the case of males (unless otherwise indicated), and to adults and subadults in the case of females.

The 20 morphometric ratios initially calculated were progressively reduced as some of them showed little variability within and between populations or phena, and others showed as much variability within populations or phena as was observed between them. Periodically all specimens were compared directly against each other at low to medium magnification (6X to 60X) to determine whether relative proportions differed conspicuously or not. Nine morphometric ratios based on 13 structures were finally found to exhibit conspicuous, apparently discontinuous, measurable differences between various phena. Those 13 structures were re-measured (at 15X), and the morphometric ratios recalculated as a check of the preliminary findings. Seven morphometric ratios based on nine measurable structures revealed the greatest discontinuities between phena, and have been chosen to diagnose and separate the taxa they represent.

In order to minimize the risk of misidentifications resulting from the usage of measuring procedures and landmarks different from those used in this study, the following guidelines as to how each structure was measured are given below:

Carapace length—maximum linear anteroposterior distance from anteriormost projections of lateral lobes to posterior margin.

Metasoma segment II length—maximum linear anteroposterior distance along frontal plane (=dorsoventral plane) from anterior apophysis of lateral submedian carina to posterior margin of segment.

Metasoma segment II width—maximum straight distance on frontal plane, and perpendicular to sagittal plane, from one lateral submedian carina to its counterpart.

Metasoma segment V length—maximum linear distance along frontal plane from anterior apophysis of lateral median carina to lateral apophysis of anal arc.

Pedipalp femur length—maximum linear distance measured along frontal plane from axial pivot of trochanter-femur articulation to dorsoexternal condyle of femur-tibia articulation.

Pedipalp femur width—maximum linear distance along frontal plane measured perpendicularly from plane tangent to internal face to the widest point on external face (usually subdistally).

Pedipalp chela length—maximum straight distance from base of digital carina (marked by a conspicuous inflection) to tip of fixed finger.

Pedipalp chela width—maximum straight distance between dorsal margin of manus and ventral margin (=ventromedian carina). Care should be exercised to ensure that both landmarks are level along the plane of measurement.

Pedipalp chela movable finger length—maximum straight distance between internal condyle of movable finger articulation and tip of finger.

To simplify cross-referencing of morphometric ratios between the various taxa, the seven ratios used below have been designated as ratios #1 through #7, and for each ratio the same designation is conserved throughout the paper.

GEOGRAPHICAL GAZETTEER

Determination of the source of origin of many of the specimens studied proved almost as challenging as the taxonomic study itself. The main source of confusion appears to be related to transliteration of Arabic names by the British and German collectors responsible for obtaining the bulk of the material examined. Existing maps and gazetteers often give different spellings for these locality names, and some names are referred to one country in the collecting labels but are in a different country at present (due to changing political boundaries in the region).

The following gazetteer (Table 1) is based largely on the Official Standard Name Gazetteer's of the various countries published by the U.S. Board on Geographic Names (U.S. Department of Interior, Washington, D.C.), and indicates: (a) locality as given in label(s) accompanying specimen(s), (b) locality as given in source above, and (c) geographical coordinates for each locality as given in the source above.

Nebo Simon

Hemiscorpio: Simon 1872:255, Karsch 1879a:15 (not *Hemiscorpio* Peters 1861).

Diplocentrus: Karsch 1879b:99 (not *Diplocentrus* Peters 1861).

Cyphocentrus Karsch 1880:408, Simon 1880b:397 (in part).

Nebo Simon 1878:399, 1879:115, 1880a:29, 1880b:398, 1883:249, 1902:254, 1910:80, Karsch 1879:22, Kraepelin 1894:14, 1899:98, 1901:270, 1905:342, Pocock 1894:357, 1896a:295, 1896b:316, 1903a:214, 1903b:202, Lonnberg 1897:197, Arldt 1908:421, Borelli 1915:462, Schenkel 1932:381, Werner 1935a:275, 1935b:211, Bodenheimer 1937:235, Shulov 1939:253, 1966:97, Vachon 1940:248, 1965:308, 1966a:766, 1966b:214, 1974:914, 1976:7, 1977:209, Whittick 1941:44, Roewer 1943:224, Shulov and Amitai 1958:351, Shulov, Rosin and Amitai 1960:65, Bucherl 1960:269, 1964:59, Rosin and Shulov 1964:547, Dresco-Derouet 1964:97, Rosin 1964:177, 1965:111, 1969a:225, 1969b:71, 1969c:75, 1972:246, 1973:107, Nitzan and Shulov 1966:17, Perez 1974:35, Williams and Lee 1975:3, Schmidt 1975:2899, Francke 1977a:95, 1978b:3.

Table 1.—Gazetteer of geographic localities where *Nebo* has been collected.

EGYPT				
Dj. Ataka	Jabal Atāqah	29° 55' N	32° 20' E	
IRAN				
Henjam	Henjām	26° 39' N	55° 53' E	
ISRAEL (West Bank of Jordan River included)				
Kaifa	Haifa	32° 50' N	35° 00' E	
Nabulus	Nābulus	32° 13' N	35° 17' E	
Wadi Jureir	Wādī Al Juraynah	32° 12' N	35° 27' E	
Maale Hachamisha	Ma 'ale Hāhamisha	31° 49' N	35° 07' E	
Jerusalem	Yerushalayim	31° 46' N	35° 14' E	
Marsaba	Mār Sābā	31° 43' N	35° 23' E	
'Ein Geddi	'En Gedi	31° 27' N	35° 23' E	
Asluj (Beer Sheva)	Asludj (Mash'Abbin Be'er)	31° 01' N	34° 46' E	
Yeruham	Yeroham	31° 00' N	34° 55' E	
Wadi Abyad	Wādī Abyad	30° 57' N	34° 24' E	
Wadi Nafkh	Wādī Nafkh (Nahāl Zin)	30° 57' N	35° 19' E	
Wadi Haleigim	Wādī Haleiqim	30° 54' N	34° 45' E	
Sde Boker or Sde Boger	Sede Boqer	30° 52' N	34° 47' E	
Ras Umm Jurfan	Rās Umm Jurfān	30° 42' N	34° 53' E	
J. Khurashe	Khurāsha (=Horesha)	30° 32' N	34° 35' E	
J. Maghara	Jebel Maghara	30° 20' N	34° 34' E	
Wadi Ajram	Wādī 'Ajramīya	30° 22' N	34° 44' E	
Aqua Bella	?	?	?	
JORDAN				
Wadi Rum	Ramm, Khawr (=Wadi)	29° 41' N	35° 27' E	
OMAN				
Dibba	Dibā	25° 38' N	56° 18' E	
Rostaq	Ar Rustāq	23° 24' N	57° 27' E	
Bait El Faley	Bayt Al Falaj	23° 37' N	58° 33' E	
Muscat or Mascate	Masqat	23° 37' N	58° 35' E	
Saiq Jekel	Sayq Jabal	16° 43' N	53° 08' E	
PEOPLES DEMOCRATIC REPUBLIC OF YEMEN (ADEN)				
Dthala	? Dal 'ah (Pass)	14° 20' N	47° 02' E	
	? Dhala (= Aq Ḍālī) (pop.)	13° 42' N	44° 44' E	
	? Dthala under Yemen Arab Republic			
Jebel Harir	Jabal Ḥarīr	13° 45' N	44° 54' E	
Shaikh Othman	Shaykh 'Uthmān	12° 52' N	44° 59' E	
Aden	'Adan	12° 46' N	45° 01' E	
Shum-Shum (Sugarloaf Mt.)	Jabal al Muzalqam	12° 45' N	44° 52' E	
SAUDI ARABIA				
Buraiman	Buraymān	21° 39' N	39° 14' E	
Qunfidan	Al Qunfudhah	19° 08' N	41° 05' E	
YEMEN ARAB REPUBLIC				
Dthala	? Thal'ah (Wādī)	16° 35' N	43° 08' E	
	? Dthala under Peoples Democratic Republic of Yemen			
Huka Hazz (or Hugga & Haz)	? Ḥāz	15° 31' N	44° 00' E	
	? Huqqah	14° 24' N	44° 30' E	
San'a (=Sanaa)	Sana	15° 21' N	44° 12' E	
Ghaiman	Ghaymān	15° 16' N	44° 21' E	
Taizz	Ta'izz	14° 47' N	44° 02' E	
Gerba	Ghirbām	14° 00' N	45° 31' E	

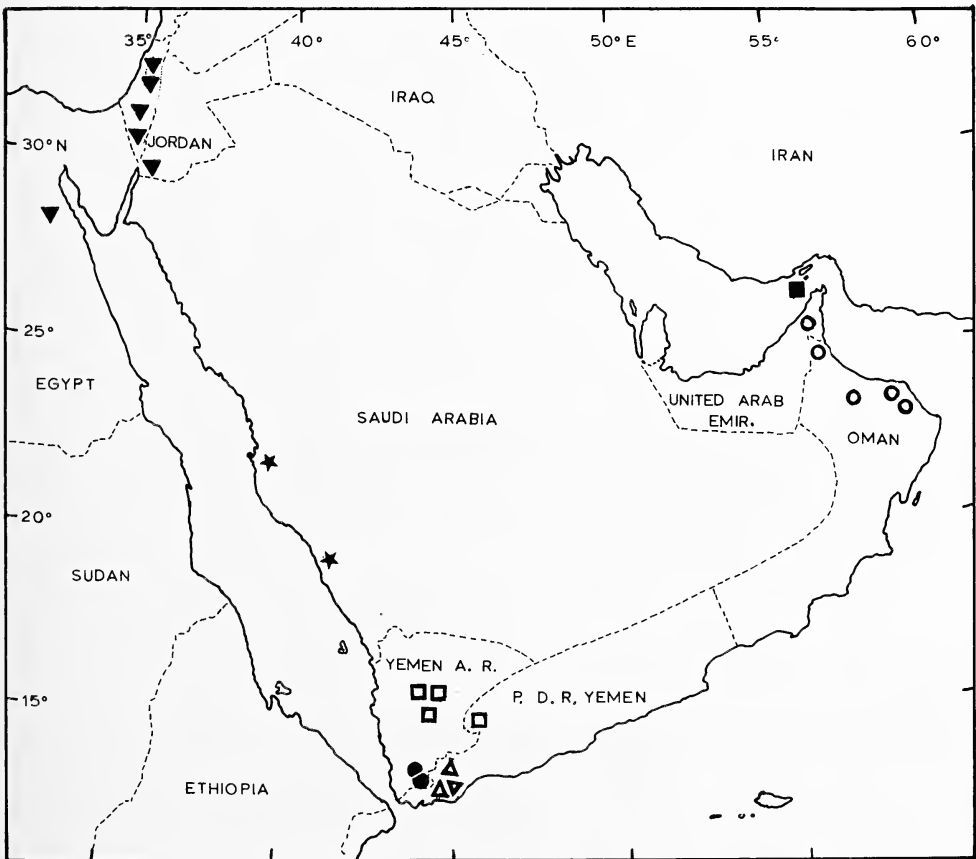
Type species.—*Hemiscorpio hierichonticus* Simon, 1872, by original designation.

Distribution.—Egypt, Iran, Israel, Jordania, Oman, Peoples Democratic Republic of Yemen, Saudi Arabia, Yemen Arab Republic (Map 1).

Diagnosis.—Sternum pentagonal. Retrolateral pedal spurs absent. Subaculear tubercle well developed, subcylindrical. Carapace with median longitudinal furrow suturiform. Orthobothriotaxia C (Vachon 1965:313, 1974:917): tibial trichobothrium d_2 on dorsal face, chelal trichobothrium it medially on fixed finger length (Francke 1977a:110).

Subordinate taxa.—*Nebo hierichonticus* (Simon), *Nebo flavipes* Simon, *Nebo grandis*, n. sp., *Nebo henjamicus*, n. sp., *Nebo omanensis*, n. sp., and *Nebo yemenensis*, n. sp.

Identification Aids.—Dichotomous keys have been avoided in this contribution for several reasons. First, due the fact that adult males are not known for two of the six species and adult females are not known for another species, and also due to the fact that considerable sexual dimorphism can occur, a single key would be very incomplete and difficult to use. Two keys, one for males and one for females, were rejected (a) because erroneous identifications could result if the unknown sex of a taxon was “forced” through the available key, and (b) because such keys tend to be monothetic or oligothetic in their characterization of the taxa. The taxa recognized below are based on a variable



Map 1.—Geographical distribution of *Nebo* spp.: *N. hierichonticus*, solid triangles; *N. flavipes*, solid circles; *N. grandis*, open triangles; *N. henjamicus*, solid square; *N. omanensis*, open circles; *N. yemenensis*, open squares; *Nebo* sp. undet., stars.

number of morphometric differences, and accurate identifications are more likely if all available differences are carefully analyzed, including geographical distributions (some taxa that are morphometrically quite similar occur at great distances from each other, while taxa that are geographically nearer to each other show considerable morphometric differences).

The morphometric characterization, based on seven ratios, of the phena (separated by sex and taxon) available appear in Table 2. Ratios useful in separating individuals of the same sex from other taxa known also from that sex appear in Table 3. Paired comparisons on the upper-right half of the matrix lead to the separation of males, while paired comparisons on the lower-left half of the matrix lead to the separation of females.

Table 2.—Morphometric characterization of adult *Nebo* spp. The seven morphometric ratios given are: 1= carapace length/metasoma segment II length, 2= pedipalp femur length/width, 3= metasoma segment V length/pedipalp chela movable finger length, 4= metasoma segment V length/carapace length, 5= metasoma segment V length/metasoma segment II width, 6= pedipalp chela length/width, 7= pedipalp femur length/pedipalp chela width.

Ratio	Sex	<i>N. hierichonticus</i>	<i>N. flavipes</i>	<i>N. grandis</i>	<i>N. henjamicus</i>	<i>N. omanensis</i>	<i>N. yemenensis</i>
1	♂	<1.45			<1.20	1.25–1.70	1.50–1.60
	♀	<1.60	>1.60	<1.60		1.25–1.70	1.60–1.70
2	♂	>2.65			>3.00	2.75–3.00	2.30–2.60
	♀	>2.65	<2.65	>2.65		2.30–2.60	2.30–2.60
3	♂	>0.90			>1.20	1.10–1.20	0.90–1.00
	♀	>0.90	<0.90	0.90–1.00		1.00–1.10	0.90–1.00
4	♂	>1.10			>1.25	1.10–1.20	1.00–1.10
	♀	>1.10	<1.10	<1.10		0.95–1.10	0.90–1.00
5	♂	>2.55			>3.10	2.60–3.10	2.30–2.55
	♀	>2.55	<2.25	>2.60		2.50–3.00	2.30–2.55
6	♂	>2.65			<2.60	2.35–2.50	2.45–2.55
	♀	>2.30	<2.30	<2.30		2.20–2.30	2.45–2.55
7	♂	>1.25			>1.25	1.20–1.30	1.20
	♀	>1.15	<1.05	<1.15		1.05–1.15	1.20

Table 3.—Identification aid matrix for adult *Nebo* spp. The numbers in the matrix refer to the ratios given in Table 2, and represent those morphometric ratios that separate the various taxa. Paired comparisons on the upper-right half of the matrix lead to the separation of males (e.g., ratios 2, 4, 5, 6 separate adult males of *N. hierichonticus* from those of *N. yemenensis*), and paired comparisons on the lower-left half of the matrix lead to the separation of females.

	<i>N. hierichonticus</i>	<i>N. flavipes</i>	<i>N. grandis</i>	<i>N. henjamicus</i>	<i>N. omanensis</i>	<i>N. yemenensis</i>
<i>N. hierichonticus</i>	XXXX			1,2,3,4,5,6,7	6	2,4,5,6
<i>N. flavipes</i>	1,2,3,4,5,6,7	XXXX				
<i>N. grandis</i>	4,6,7	1,3,5	XXXX			
<i>N. henjamicus</i>				XXXX	1,2,3,4,5	1,2,3,4,5
<i>N. omanensis</i>	6,7	1,3,5,7	2,3		XXX	2,3,4,5
<i>N. yemenensis</i>	2,4,5	3,5,6,7	1,2,5,6,7		3,6,7	XXXX

Nebo hierichonticus (Simon)
Figs. 1-2.

Hemiscorpio hierichonticus Simon 1872:255, Karsch 1879a:15.
Nebo hierichonticus: Simon 1878:399, 1880a:29, *nec* 1902:254, 1910:81, Karsch 1879a:22, Pocock 1903:214, *nec* Whittick 1941:44, Shulov and Amitai 1958:351, Rosin 1964:177, 1969a:225, 1969b:71, 1969c:75, 1972:246, 1973:107, Nitzan and Shulov 1966:17, Vachon 1966a:766, 1966b:214 (in part), 1974:915, 1976:7, *nec* Vachon 1977:211, Schimdt 1975:2899.
Nebo hierochonticus (sic): Kraepelin 1894:14 (in part), 1899:98 (in part), *nec* 1901:270, Borelli 1915:462 (in part ?), Schenkel 1932:381, Werner 1935a:275 (in part), 1935b:211, Bodenheimer 1937:235, *nec* Finnegan 1932:92, *nec* Roewer 1943:224, Bücherl 1960:269, Shulov et al. 1960:65, Rosin and Shulov 1963:547 (in part), Dresco-Derouet 1964:97, Vachon 1965:308 (in part), Rosin 1965:111, Shulov 1966:97, Perez 1975:35 (in part).
Nebo hierochunticus (sic): Simon 1879:115.
Nebo hiericonticus (sic): Shulov 1939:253.
Nebo hieronchonticus (sic): Bücherl 1964:59.
Nebo hierichanticus (sic): Abushama 1968:37.
? *Diplocentrus sulcatus* Karsch 1879b:99.
? *Cyphocentrus sulcatus*: Karsch 1880:407.

Type data.—Holotype of *hierichonticus*, juvenile male (RS 1181), allotype juvenile female (RS 3493), and paratype juvenile male (RS 3490), from the Jordan Valley, “Syrie”, no date (Ch. de la Brulerie), Museum National d’Histoire Naturelle, Paris, examined. Two syntypes of *sulcatus*, from “Africa”, could not be located and might be lost or destroyed as is the case with a number of Karsch’s types.

Distribution.—Egypt, Israel, Jordan (Map 1).

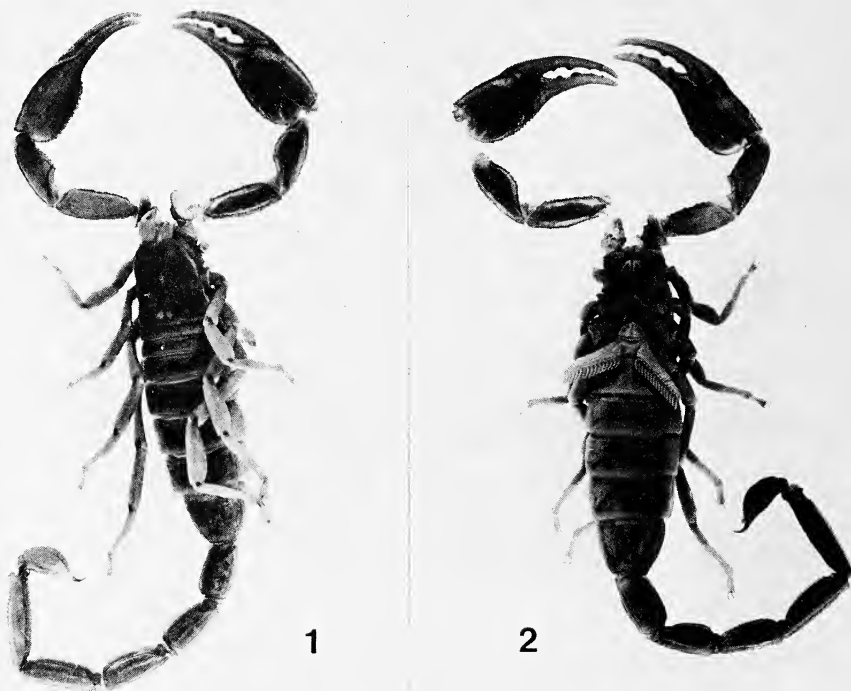
Diagnosis.—Adults 85-110 mm long (Table 4). Pectinal tooth count 14-20 (mode 18) on males, 12-16 (mode 14) on females. Carapace length/metasoma segment II length ratio (#1) considerably less than 1.70, pedipalp femur length/width ratio (#2) greater than 2.65, metasoma segment V length/pedipalp chela movable finger length ratio (#3) greater than 0.90, metasoma segment V length/carapace length ratio (#4) greater than 1.10, metasoma segment V length/metasoma segment II width ratio (#5) greater than 2.50, pedipalp chela length/width ratio (#6) greater than 2.65 in adult males, greater than 2.30 in females, pedipalp femur length/pedipalp chela width ratio (#7) greater than 1.25 in males, greater than 1.15 in females.

Table 4.—Measurements (in millimeters) of *Nebo hierichonticus* (Simon) and *Nebo flavipes* Simon.

	<i>Nebo hierichonticus</i>			<i>Nebo flavipes</i>		
	Lectotype	Adult ♂	Adult ♀	Lectotype	Adult ♀	Adult ♀
	Subadult ♂	(Jordania)	(Jordania)	Subadult ♂	“Marsaba”	Yemen
Total length	64.2	87.8	105.2	79.1	95.8	97.5
Carapace length	8.9	10.7	12.7	10.5	13.7	13.3
Metasoma II length	5.0	7.8	7.9	6.3	7.8	7.7
width	3.8	4.8	5.0	5.0	6.1	5.5
Metasoma V length	7.6	12.2	14.1	9.1	11.4	12.2
width	3.0	3.8	3.3	3.9	4.5	4.0
Pedipalp femur length	6.7	10.7	12.4	8.6	10.8	11.0
width	3.0	3.9	4.6	4.0	4.9	4.6
Pedipalp chela length	14.5	21.9	23.8	18.9	23.8	24.0
width	5.4	7.7	10.0	7.7	11.0	11.0
Movable finger length	8.8	13.0	13.5	11.6	14.8	13.7
Pectinal tooth count	15-16	15-16	14-14	18-18	15-14	16-15

Comparisons.—Ratios #4 and #6 above, singly or in combination, will separate *N. hierichonticus* from all other congeneric species. Additional differences with specific taxa will be given as those taxa are treated.

Specimens examined.—**EGYPT:** Jabal Atāqah, February 1889 (no coll.), 1 imm. male (MNHN). **ISRAEL:** Jordan Valley, no date (Ch. de la Brulerie), 2 imm. males, 1 imm. female (MNHN), Haifa, 1 February 1901 (no coll.), 1 male (ZMH), Nabulus, 21 February 1897 (P. Born), 1 female (ZMH), Wadi Al Juraynah, 1 April 1955 (Levitas), 1 imm. female (MNHN), Ma'ale Hāhamisha, 3 November 1958 (P. Amitai), 1 imm. male (AMNH), Jerusalem, 1873 (Schneller), 1 female (ZMH), Mār Sābā, no date (M. A. Letourneux), 1 male (MNHN), 'En Gedi, 8 April 1951 (J. Warhman), 1 female, 14 March 1953 (J. Warhman), 5 imm. males, 3 imm. females (MNHN), Asludj, 30 January 1954 (Werner), 1 imm. male (MNHN), Yeroḥam, 5 April 1954 (Werner), 1 imm. female (MNHN), Wādī Abyad, 25 March 1952 (J. Warhman), 1 female, 3 imm. males, 3 imm. females (MNHN), Wādī Nafkh, 25 February 1949 (J. Warhman), 1 female (MNHN), Wādī Haleiqim, 25 September 1952 (J. Warhman), 1 imm. male (MNHN), Sede Boqer, March 1953 (J. Warhman), 1 female (MNHN), 2 March 1955 (Werner), 2 imm. males, 1 imm. female (MNHN), Rās Umm Jurfān, 28 November 1949 (J. Warhman), 1 imm. male, 1 imm. female (MNHN), Khurāsha, 1 April 1955 (Levitas), 2 imm. males, 2 imm. females (MNHN), Jebel Maghara, 1 April 1955 (Levitas), 1 imm. male (MNHN), Wādī 'Ajramī ya, 29 February 1949 (J. Warhman), 1 imm. male (MNHN), Aqua Bella, 10 May 1950 (J. Warhman), 1 imm. male (MNHN), Negev, 1952 (J. Warhman), 1 imm. male (MNHN). **JORDAN:** Jordan, no date (no coll.), 1 imm. male (MNHN), Ramm Khawr, April 1975 (B. and P. Lanza), 1 female, 1 imm. male, 1 imm. female (Firenze), Avdat, Negev Desert, no date (no coll.), one imm. male (ENKW).



Figs. 1-2.—*Nebo hierichonticus* (Simon), adult male from Mar Saba, Israel: 1, dorsal view; 2, ventral view.

Nebo flavipes Simon

Figs. 3-4

Nebo flavipes Simon 1883:249, *nec* Pocock 1896a:295, 1896b:316, 1903a:214 (in part), Kraepelin 1899:98, *nec* 1901:270, Werner 1935b:211, *nec* Bodenheimer 1937:235, Vachon 1940:250 (in part ?), 1965:308.

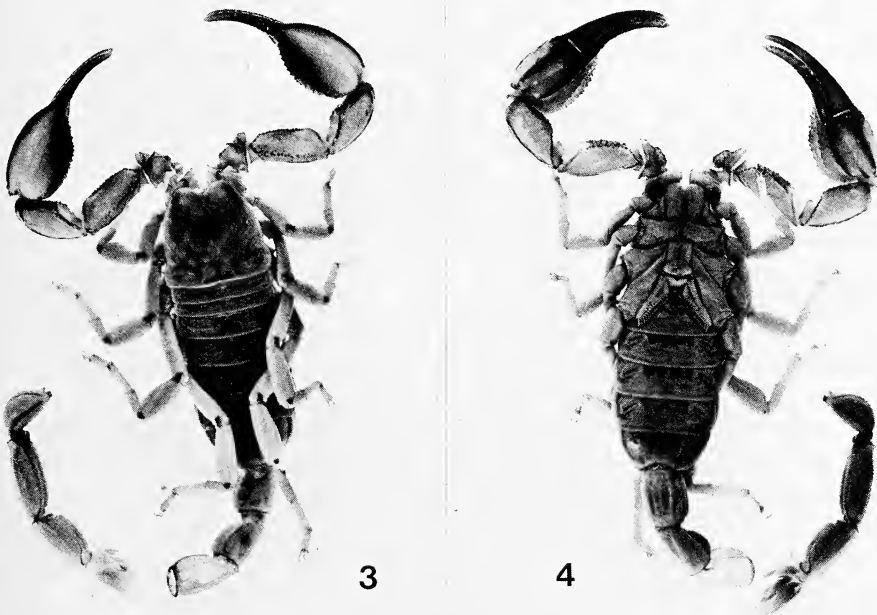
Nebo hierichonticus (in part): Kraepelin 1894:14, Werner 1935a:275, Whittick 1941:44, Roewer 1943:224, Rosin and Shulov 1963:547, Vachon, 1966b:214, Perez 1974:35.

Nebo hierichonticus pallidimanus Pocock 1903a:214, Perez 1974:35. NEW SYNONYMY.

Type data.—Holotype of *flavipes*, immature male, from Ta'izz, Yemen Arab Republic, no date (R. Manzoni), Museum National d'Histoire Naturelle, Paris, examined. Lectotype of *hierichonticus pallidimanus*, adult female hereby designated, from Ghirbām, Yemen Arab Republic, no date (G. W. Berry), British Museum (Natural History), London, examined.

Distribution.—Yemen Arab Republic, Peoples Democratic Republic of Yemen? (Map 1). See Remarks.

Diagnosis.—Adult females 90-100 mm long (Table 4), adult males unknown. Pectinal tooth count 16-20 (mode 18) on males, 14-16 (mode 15) on females. Carapace length/metasoma segment II length ratio (#1) greater than 1.70, metasoma segment V length/pedipalp chela movable finger length ratio (#3) less than 0.90, metasoma segment V length/metasoma segment II width ratio (#5) less than 2.25, pedipalp femur length/pedipalp chela width ratio (#7) less than 1.20 in males, less than 1.05 in females.



Figs. 3-4.—*Nebo flavipes* Simon, adult female from Mar Saba, Israel (see discussion in text): 3, dorsal view; 4, ventral view.

Comparisons.—Ratios #1, #3, #5, and #7 above separate *N. flavipes* from all other congeneric species. Ratios #2, #4, and #6, given in the diagnosis of *N. hierichonticus* also separate this taxon from *N. flavipes*. Additional differences between *N. flavipes* and the new species described below appear in the comparisons' sections of the latter.

Specimens examined.—**YEMEN ARAB REPUBLIC:** Ta'izz, no date (R. Manzoni), holotype male and immature male paratype of *flavipes* (MNHN), Ghirbām, no date (G. W. Berry), one adult female (designated lectotype) and one subadult female of *hierichonticus pallidimanus* (BM). **P. D. R. of YEMEN (?)**: Aden, no date (Marquis G. Doria), subadult male and subadult female "co-types" of *flavipes* (BM). **OTHERS:** Syrie, Mār Sābā (M. Letourneux), one adult female (MNHN), no locality, no date (F. W. Townsend), one subadult male (BM), no locality, October 1912 (no coll., Mus. Calcutta), one imm. male (ZMH).

Remarks.—Only the specimens from Yemen Arab Republic seem to have accurate locality data. The "co-types" of *flavipes* from "Aden" could be from the city of that name (although it is doubtful since a different species occurs there), or from the country of P. D. R. of Yemen (formerly known as Aden). The female from Mār Sābā, Syrie, is accompanied by an adult male *N. hierichonticus*, to whom the locality data most likely applies; the female was probably collected somewhere else, considered conspecific to the male and subsequently placed in the same jar.

Nebo grandis, new species

Figs. 5-6

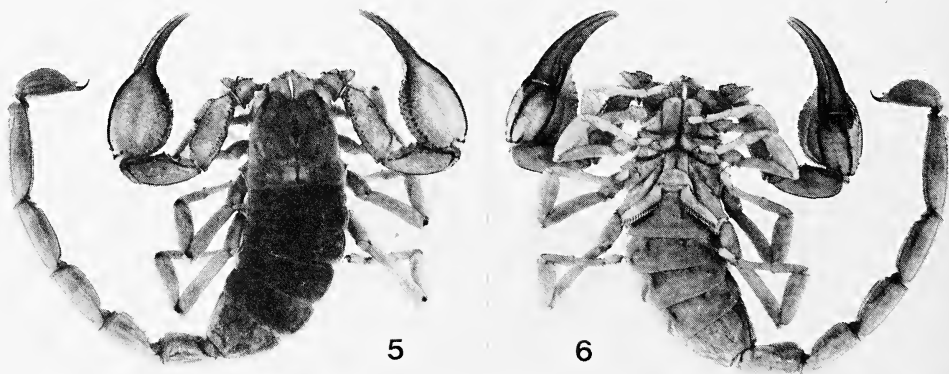
Nebo hierichonticus: Whittick 1941:44 [misidentification; specimens from Dhala, Western Aden Protectorate (=Yemen Arab Republic) only].

Nebo flavipes: Pocock 1896b:316 [misidentification].

Type data.—Holotype female, adult, from "Dthala (Yemen) Arabia, no date (G. W. Berry)"; British Museum (Natural History), London. See gazetteer for possible geographical positions of this locality.

Etymology.—Specific name from the Latin *grandis*, meaning large. Adults of this species attain the largest size observed in the genus.

Distribution.—Peoples Democratic Republic of Yemen, Yemen Arab Republic ? (Map 1).



Figs. 5-6.—*Nebo grandis*, n. sp., adult female from Dthalla, P. D. R. Yemen: 5, dorsal view; 6, ventral view.

Diagnosis.—Adult females 120-145 mm long (Table 5), adult males unknown. Pectinal tooth counts 17-19 in males, 14-16 in females. Carapace length/metasoma segment II length ratio (#1) less than 1.60, metasoma segment V length/pedipalp chela movable finger length ratio (#3) greater than 0.90, less than 1.00; metasoma segment V length/metasoma segment II width ratio (#5) greater than 2.60, pedipalp chela length/width ratio (#6) less than 2.30, pedipalp femur length/pedipalp chela width ratio (#7) less than 1.15.

Comparisons.—Adult females of *N. grandis* can be separated from adult *N. hierichonticus* females by ratios #6 and #7 as indicated in their respective diagnoses. Presumed subadult males of *N. grandis* (92 mm and 81 mm long respectively) differ from adult and subadult *N. hierichonticus* as follows (morphometric statements refer to *grandis*, the alternate condition occurs in *hierichonticus*): metasoma segment V length/pedipalp chela movable finger length ratio (#3) less than 0.90, metasoma segment V length/metasoma segment II width ratio (#5) less than 2.55, and pedipalp chela length/width ratio (#6) less than 2.65.

Adult females of *N. grandis* can be separated from adult *N. flavipes* females by ratios #1, #3 and #5 as indicated in their respective diagnoses. In addition, the pedipalp femur length/width ratio (#2) in *N. flavipes* is less than 2.45, and in *N. grandis* is greater than 2.45. Subadult males of these two species differ as follows (morphometric statements refer to *N. grandis*, the alternate condition occurs in *N. flavipes*): metasoma segment V length/pedipalp chela movable finger length ratio (#3) greater than 0.80, metasoma segment V length/carapace length ratio (#4) greater than 0.90, and metasoma segment V length/metasoma segment II width ratio (#5) greater than 2.25.

Specimens examined.—PEOPLES DEMOCRATIC REPUBLIC OF YEMEN (ADEN): Dthala, no date (G. W. Berry), holotype female (BM), Dthalla, no date (Capt. H. R. Watson), two adult females (BM), “halfway up small mt. summit of Shum Shum” (=Jabal al Muzalqam) (Col. Yerboung), one subadult and one imm. male (BM), Shaykh ‘Uthmān, 9 February 1895 (? , label=9.2.95) (no coll.), one subadult male (BM), Aden (city?), no date (no coll.) one imm. male (MNHN).

Table 5.—Measurements (in millimeters) of *Nebo grandis*, n. sp., *Nebo henjamicus*, n. sp., *Nebo omanensis*, n. sp., and *Nebo yemenensis*, n. sp.

	<i>grandis</i>		<i>henjamicus</i>	<i>omanensis</i>		<i>yemenensis</i>	
	Holotype	Subadult ♂	Holotype	Holotype	Adult ♀	Holotype	Adult ♂
	Adult ♀	Aden	Adult ♂	Adult ♂	Oman	Adult ♀	Yemen
Total length	142.4	92.6	122.3	111.0	101.0	88.2	80.2
Carapace length	18.4	11.6	13.2	12.9	12.2	11.2	10.2
Metasoma II length	11.7	7.5	11.2	9.4	8.2	6.8	6.8
width	6.9	4.8	5.0	5.2	4.4	4.3	4.3
Metasoma V length	18.4	11.5	17.3	14.9	13.0	10.9	10.4
width	4.9	3.7	3.7	4.1	3.4	3.3	3.3
Pedipalp femur length	14.9	10.1	13.6	12.9	10.9	9.5	9.6
width	6.2	4.1	4.4	4.4	4.2	3.9	3.8
Pedipalp chela length	32.0	21.0	25.6	24.8	21.9	19.1	18.5
width	14.2	8.6	10.1	10.5	9.8	7.7	7.4
Movable finger length	19.6	13.0	14.0	13.0	12.4	10.9	10.4
Pectinal tooth count	14-15	18-19	19-20	21-22	14-14	13-13	15- ?

Nebo henjamicus, new species

Figs. 7-8

Nebo hierichonticus: Whittick 1941:44 [misidentification; specimen from "Henjam on the Persian Gulf" only].

Type data.—Holotype, adult male from Iran, island of Henjam in the Persian Gulf, 8 March 1931 (Lt. Commander R. A. Stephens), British Museum (Natural History), London.

Etymology.—Specific name based on the type locality.

Distribution.—Known only from the type locality (Map 1).

Diagnosis.—Holotype, and only known specimen, 122 mm long (Table 5). Pectinal tooth count 19-20. Carapace length/metasoma segment II length ratio (#1) less than 1.20, pedipalp femur length/width ratio (#2) greater than 3.00, metasoma segment V length/pedipalp chela movable finger length ratio (#3) greater than 1.20, metasoma segment V length/carapace length ratio (#4) greater than 1.25, metasoma segment V length/metasoma segment II width ratio (#5) considerably greater than 3.00, pedipalp femur length/pedipalp chela width ratio (#7) greater than 1.25.

Comparisons.—*Nebo henjamicus* can be separated from adult *N. hierichonticus* males by ratios #1, #2, #3, #4, #5, and #7 as given above. Furthermore, the pedipalp chela length/width ratio (#6) in *N. henjamicus* is less than 2.60, while it is greater than 2.65 in *N. hierichonticus*. It differs from *N. flavipes* by ratios #1, #2, #3, #4, #5 and #7 as given above. Finally, it differs considerably from subadult *N. grandis* males in ratios #3 (less than 0.90 in *grandis*), #4 (less than 1.00 in *grandis*) and #5 (less than 2.55 in *grandis*).

Specimens Examined.—IRAN: island of Henjam in the Persian Gulf, 8 March 1931 (Late Lt. Commander R. A. Stephens, R. N. on HMS "Ormande"), holotype male (BM).



Figs. 7-8.—*Nebo henjamicus*, n. sp., holotype male from Henjam, Iran: 7, dorsal view; 8, ventral view.

Nebo omanensis, new species

Figs. 9-10

Nebo hierichonticus: Kraepelin 1901:270, Simon 1902:254, Vachon 1977:211 (misidentifications).
Nebo flavipes: Pocock 1896a:295 (part), 1903a:214 (part), Kraepelin 1901:270 (part) (misidentifications).

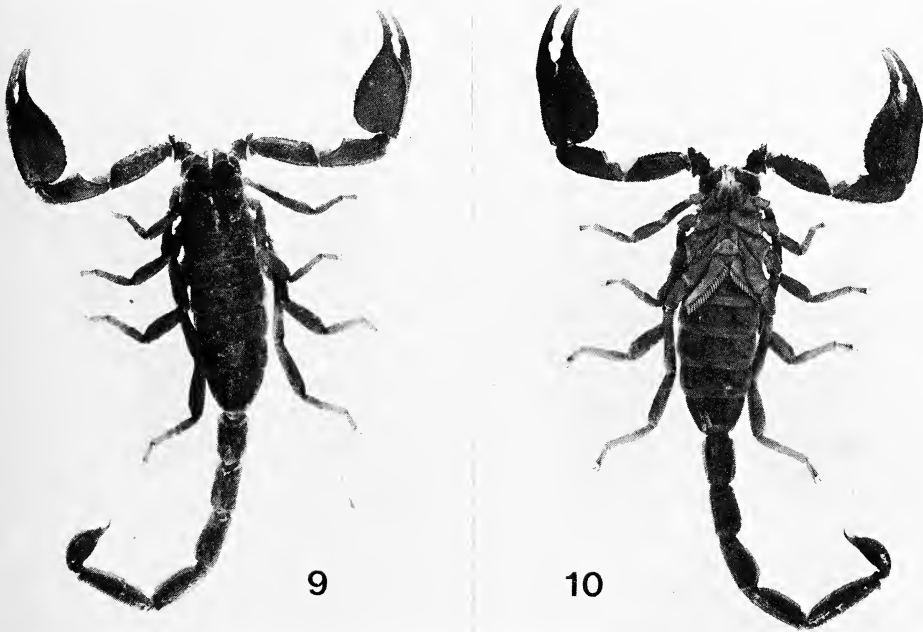
Type data.—Holotype, adult male, from Oman, Bayt Al Falaj, August 1916 (Maj. Burton); British Museum (Natural History), London.

Etymology.—Specific name based on the country in which this species occurs.

Distribution.—Oman, United Arab Emirates ? (Map 1).

Diagnosis.—Adult males 95-115 mm long, adult females 90-105 mm long (Table 5). Pectinal tooth counts 17-22 (mode 20) in males, 14-17 (mode 15) in females. Carapace length/metasoma segment II length ratio (#1) greater than 1.25, less than 1.70; pedipalp femur length/width ratio (#2) 2.75-3.00 in males, 2.30-2.60 in females; metasoma segment V length/pedipalp chela movable finger length ratio (#3) 1.10-1.20 in males, 1.00-1.10 in females; metasoma segment V length/carapace length ratio (#4) 1.10-1.20 in males, 0.95-1.10 in females; metasoma segment V length/metasoma segment II width ratio (#5) 2.60-3.10 in males, 2.50-3.00 in females; pedipalp chela length/width ratio (#6) 2.35-2.50 in males, 2.20-2.30 in females; pedipalp femur length/pedipalp chela width ratio (#7) 1.20-1.30 in males, 1.05-1.15 in females.

Comparisons.—Morphometrically *N. omanensis* is very close to *N. hierichonticus*, the most significant difference lying in the relative width of the pedipalp chela: adult males can be separated by ratio #6, and adult females by ratios #6 and #7 as indicated in their respective diagnoses. Adult *N. omanensis* can be separated from adult *N. flavipes* by ratios



Figs. 9-10.—*Nebo omanensis*, n. sp., adult male from Sayq Jabal, Oman: 9, dorsal view; 10, ventral view.

#1, #3, #5 and #7 as indicated in their respective diagnoses. Adult females of *N. omanensis* differ from adult females of *N. grandis* in size and in ratio #3 as indicated in their respective diagnoses. Subadult males of *N. grandis* differ from adult *N. omanensis* males in ratios #3 and #5 as indicated above and in the comparisons' section of *N. grandis*. Finally, adult *N. omanensis* males differ from *N. henjamicus* in ratios #1, #2, #3, #4 and #5 as indicated in their respective diagnoses.

Specimens examined.—OMAN: Bayt Al Falaj, August 1916 (Maj. Burton), holotype male and subadult female (BM); near Ar Rustāq, 12 April 1975 (M. S. and J. Baddeley), one adult male and one adult female (Mus. Oman); Sayq Jabal (Persian Gulf), 16 July ??? (Major M. D. Gallagher), one adult male, two females, one imm. male (BM); Muscat, no date (A. G. Jayakar), one adult male and one imm. female (BM); Dibā (Persian Gulf), March-April 1901 (no coll.), one imm. female (MNHN); Mascate, October-November 1896 (no coll.), one adult male, three imm. males, five imm. females (MNHN). Additional locality records in Oman appear in Vachon (1977:211).

Nebo yemensis, new species

Figs. 11-12

Nebo hierichonticus: Kraepelin 1894:14 (in part), Whittick 1941:44 (in part), Roewer 1943:224 (misidentifications).

Type data.—Holotype, adult female, from Yemen Arab Republic, 15 miles NW Sana, under stones at top of El Kabar Pass between Hugga and Haz (ca. 9,200 ft.), 2 February 1938 (E. B. Britton; British Museum Expedition to SW Arabia); British Museum (Natural History), London.

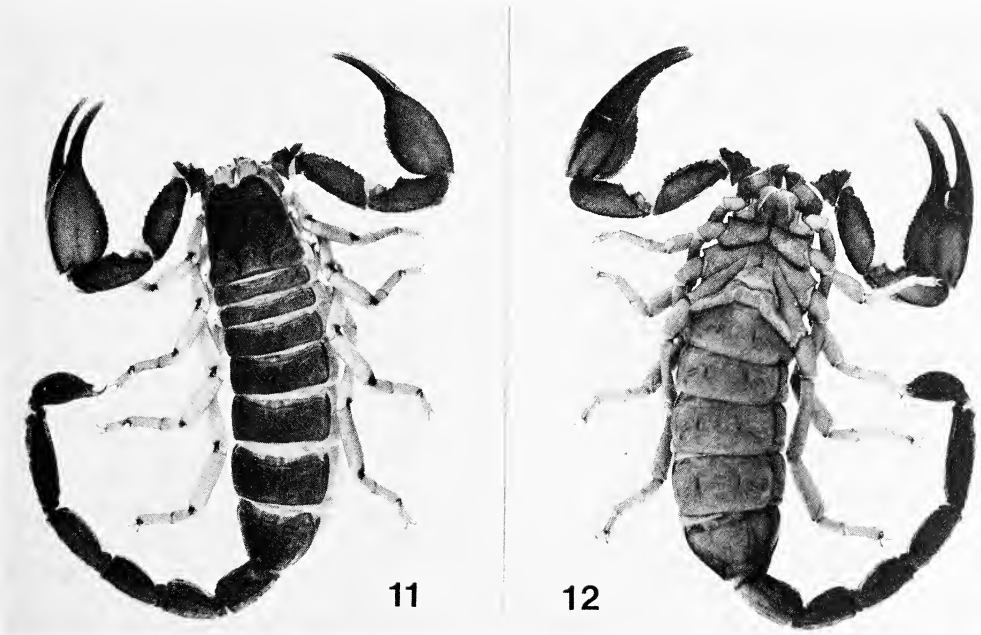
Etymology.—Specific name based on the countries in which this species occurs.

Distribution.—Peoples Democratic Republic of Yemen, Yemen Arab Republic (Map 1).

Diagnosis.—Adult males 80-90 mm long, females 85-100 mm long (Table 5). Pectinal tooth counts 15-18 (mode 16-17) in males, 13-16 (mode 14) in females. Carapace length/metasoma segment II length ratio (#1) 1.50-1.60 in males, 1.60-1.70 in females; pedipalp femur length/width ratio (#2) 2.30-2.60; metasoma segment V length/pedipalp chela movable finger length ratio (#3) 0.90-1.00; metasoma segment V length/carapace length ratio (#4) 1.00-1.10 in males, 0.90-1.00 in females; metasoma segment V length/metasoma segment II width ratio (#5) 2.30-2.55; pedipalp chela length/width ratio (#6) 2.45-2.55; pedipalp femur length/pedipalp chela width ratio (#7) greater than 1.20.

Comparisons.—Adult *Nebo yemensis* can be separated from adult *N. hierichonticus* by ratios #2, #4 and #5 (and for males only ratio #6 also); from adult *N. flavipes* by ratios #1, #3, #5 and #7; from adult female *N. grandis* by ratios #5, #6 and #7, and from subadult male *N. grandis* by ratios #3 and #4; from adult *N. henjamicus* male by ratios #1, #2, #3, #4 and #5; and from adult *N. omanensis* males by ratios #2, #4 and #5, and from females by ratios #6 and #7, as indicated in each species' respective diagnosis.

Specimens examined.—YEMEN ARAB REPUBLIC: 15 miles NW Sana, under stones at top of El Kabar Pass between Hugga and Haz (ca. 9,200 ft.), 2 February 1938 (E. B. Britton), adult holotype female and adult paratype female (BM); Huka-Hazz, 1-7 February 1928 (no coll.), one adult female and two imm. females (ZMH); Sana, 1-7 September 1931 (Dr. C. Rathjens), three imm. males and two imm. females (ZMH); Sana (about 7,900 ft.) 8 December 1937 (Dr. Carl Rathjens), one adult male (BM); Wadi Dhahr, 6 miles NW Sana (7,900 ft.), 5 February 1938 (E. B. Britton), one subadult male and one imm. female (BM); Ghaiman nr. Sana (ca. 9000 ft.), 17 February 1938 (E. B. Britton), two imm. males (BM). PEOPLES DEMOCRATIC REPUBLIC OF YEMEN: Jebel Harir, October 1937 (E. B. Britton and H. Scott), one imm. male and two imm. females (BM).



Figs. 11-12.—*Nebo yemenensis*, n. sp., holotype female from El Kabbar Pass, Yemen Arab Republic: 11, dorsal view; 12, ventral view.

Nebo, undetermined species

The following specimens from Saudi Arabia could not be assigned to a specific taxon due to the lack of adequate samples. The single adult female available is morphometrically closer to *N. hierichonticus* on some ratios, and closer to *N. yemenensis* in others. Additional adult specimens, including males are needed before their status can be determined. Their distribution, however, is important in that it tends to reduce the otherwise apparent geographical discontinuity between *N. hierichonticus* and all the other species (Map 1).

Specimens examined.—**SAUDI ARABIA:** Buraiman, north of Jiddah, 2 August 1949 (J. Hewitt), one adult female (BM), Qunfidan, 7 January 1945 (L. A. Tillin), one imm. male (BM), Arabie, 1884 (no coll.), one imm. female (MNHN).

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ATTITUDE CHANGE OF *NEPHILA CLAVIPES* SPIDERLINGS (ARANEAE: ARANEIDAE) DURING COMMUNAL LIFE¹

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ABSTRACT

Orientation of the body with respect to gravity by *Nephila clavipes* (L.) spiderlings were scored from the beginning of emergence from the egg sac until the onset of dispersion in the laboratory. Most second instar spiderlings adopted the dorsal-down attitude by the end of the seventh day. A change from dorsal-down to anterior (face)-down attitude—that of spiders living in geometric webs—was apparent on the eighth day, by third instar animals after they had completed the second molt and returned to the communal web. The anterior-down attitude predominated by the time dispersion began.

INTRODUCTION

The orientation of the body of an orb weaving spider with respect to gravity—its attitude—is so commonplace that it often escapes close attention. Bristowe (1958) describes *Araneus diadematus* Clerck as "... sitting head downward in the center of her exquisite orb. . . ."; although many familiar books about spiders have pictures confirming this attitude as typical of the orb weaver, there are few descriptions or studies of it. Considering that the web is a vital extension of its builder (cf., Savory 1952:20, Witt 1975), the attitude of the spider in the web center should not remain ignored.

Our attention was drawn to this topic while observing behavior changes associated with the onset of dispersion and geometric web building in golden silk spiderlings, *Nephila clavipes* (L.). Most solitary spiders, including *Nephila*, live together in the egg sac, and commonly thereafter in a tangle of silk for some time after hatching; dispersion is accompanied by changes in behavior (Wilder 1868, McCook 1890, Bristowe 1939, Tolbert 1977). These changes in *Nephila* spiderlings in the laboratory are radical and begin to appear shortly after the second molt (Kimmel and Grant, unpubl. data). Among these changes is the adoption of the head down attitude characteristic of adults at rest, except when posture is adjusted for thermoregulation (Krakauer 1972, Robinson and Robinson 1974). This paper documents the attitude changes that precede dispersion of *Nephila clavipes* spiderlings.

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MATERIALS AND METHODS

Nephila clavipes spiderlings (approximately 425) emerged from an egg sac collected in March 1978 on the South Carolina coast. They formed their communal tangle web, at the top of a 61 x 61 x 9 cm (h x w x d) observation cage containing branches in the laboratory, on 28 March. The cage remained at room temperature (21 - 25° C) and was exposed to a photoperiod (shifted back about 3 hr) of 13 hours of light, from above and a nearby window, and 11 hours of darkness each day. A light mist of water was applied after morning observations and again each evening. Food was not supplied, and the animals were otherwise left undisturbed. Data were collected in 38 scoring periods during ten of the 11 days between beginning of emergence from the egg sac and the onset of dispersion 12 days later (28 March through 7 April, at Davidson, N. C., 35.50° N lat.). Observations were made during the first hour of light each day, and for a longer period in the morning of days 2, 9, and 11, and in the afternoons and/or evenings on days 1, 6, and 8-11.

Spiderlings were selected for scoring from among those not tightly grouped together, in lower parts of the communal mass or on branches during migration. Only animals at rest and whose attitudes could be clearly discerned were scored: a different number of animals was scored each period. Attitude was estimated by eye, with the aid of a protractor when necessary. Any spiderling resting head down, with the anteroposterior body axis no more than $\pm 30^\circ$ from vertical was designated "anterior" attitude ($60/360 = 0.167$ chance of scoring this attitude). Any animal resting with the frontal plane of its body within $\pm 30^\circ$ of horizontal was scored either "dorsal" or "ventral," depending upon whether its dorsum or its venter was closer to the center of the earth ($120/360 \times 0.5 = 0.167$ expected frequency of either attitude by chance alone). Any animal fitting into none of the above categories (that is, with the long axis of its body more than $\pm 30^\circ$ from vertical and its frontal plane more than $\pm 30^\circ$ from horizontal) lay with its side or its posterior surface down and was scored "lateral" (chance frequency 0.5).

Data were combined from observations made during each light period, and the frequencies of each attitude calculated. Daily frequencies were ranked and used in calculating Spearman's rho, or rank correlation coefficient (Conover 1971), and Cooper's sum (Cooper 1975), non-parametric tests for increasing or decreasing trend. Daily frequencies

Table 1.—Daily frequencies of the four attitudes of spiderlings from the time of emergence (day 1) until dispersion began (day 12). The second molt, distinguishing the second instar from the third, began on day 8.

Attitude	Day, post emergence									
	1	2	3	4	6	7	8	9	10	11
	Second instar spiderlings					Third instar				
Ventral	0.00	0.02	0.00	0.00	0.03	0.00	0.02	0.03	0.00	0.00
lateral	0.48	0.47	0.51	0.39	0.25	0.23	0.23	0.04	0.16	0.12
dorsal	0.42	0.42	0.43	0.47	0.65	0.58	0.35	0.28	0.15	0.21
anterior	0.10	0.09	0.06	0.14	0.07	0.19	0.40	0.65	0.69	0.67
No. observ. periods	3	3	2	1	2	1	4	7	5	3
No. animals scored	88	64	51	28	60	31	48	68	88	52

of each attitude were corrected for weighting in scoring and the chi-square test for random attitude distribution applied.

Notes were kept on the times of emergence, migration, communal life, molting, and dispersion. *Nephila clavipes* spiderlings usually molt once in the egg sac (Grant, unpubl, data). Spiderlings are termed second instar after completion of this molt. Third instar animals are those that have completed the second molt, which occurs near the communal tangle.

RESULTS

The frequencies of spiderlings found each day in each of the four attitudes are given in Table 1, and are graphed as the distance between lines in Fig. 1. None appears to change through the first three post-emergence days, the period when most of the spiderlings were migrating to form the communal tangle. Frequencies of animals resting in the lateral attitude decreased over the span of the observations. Frequencies of second instar spiderlings adopting the dorsal attitude increased with time: the dorsal attitude was the predominant attitude of second instars by the end of the seventh day, after which the second molt began. Frequencies of second instar spiderlings in the anterior attitude remained low and changed little. Most third instar animals rested in the anterior attitude. The change in attitude from predominantly dorsal to predominantly anterior was abrupt

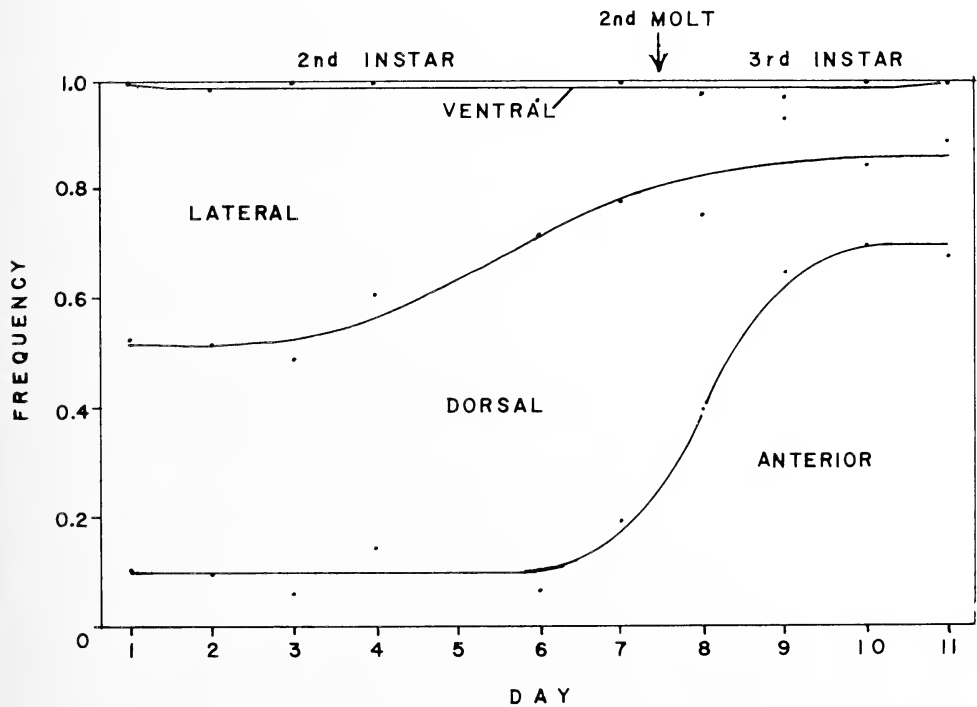


Fig. 1.—Distribution of attitude frequencies on the days between emergence (day 1) and the onset of dispersion (day 12). The four attitude frequencies for each day, from Table 1, are plotted successively on the vertical axis: each frequency is thus represented by the distance between the curves or edges of the graph bounding it.

and clearly apparent on the eighth day, the day third instar spiderlings were first present. Anterior attitude frequencies continued to increase thereafter.

All of these changes in attitude during the second and third instars are statistically significant ($P < 0.05$) by both tests for trend (Table 2). Attitude distribution was random at no time over the course of the observations: chi-square tests for random distribution among the four attitudes, or among the three predominant attitudes, gave P values < 0.005 for each day and for both instars.

DISCUSSION

Nephila clavipes spiderlings undergo changes in attitude during communal life in the laboratory, before the onset of dispersion. Most have adopted the dorsal attitude by the end of the second instar. Third instar spiderlings rest primarily in the anterior attitude. The change in predominant attitude from dorsal to anterior is associated with the second molt. Many spiderlings came to rest head down when they first returned to the communal tangle after completion of the second molt. The attitude change precedes dispersion by at least three days. Numerous observations of subadult and adult *Nephila* confirm both that the anterior attitude is the one typically adopted as they rest in the hubs of geometric webs (Wilder 1868, Robinson and Robinson 1973) and that $\pm 30^\circ$ from vertical are generous limits (Grant and Kimmel, unpubl. observations).

Orb weaving spiders sense and respond to gravity. Newly emergent spiderlings, for example, are negatively geotactic (McCook 1890, Burch 1979) and spiderling attitude is not random in the laboratory. Orb webs are placed in space with reference to gravity (Kaston 1964, Witt *et al.* 1977). Behavioral responses to gravity may be modified by other environmental circumstances, however. Mature *Nephila clavipes* females may face their webs south in winter (Carrel 1978), and alter their postures when exposed to direct sunlight (Krakauer 1972, Robinson and Robinson 1974). Gravity-oriented behavior seems to be an inherited phenotype that the animal can alter in the field for thermoregulation at least.

We are tempted to speculate about the importance of the attitude change described herein to the subsequent appearance of the behavior displayed by orb weavers as they build and use geometric webs, and to the puzzles of phylogenetics, physiology of geotaxis

Table 2.—Spearman's and Cooper's tests for trend applied to ranked daily frequencies of spiderlings in dorsal, lateral, and anterior attitudes. Frequencies ranked in increasing or decreasing order over second instar (2), third instar (3), or the entire eleven days of observations.

Attitude	Days	Instar	Trend	Spearman's rho	P	Cooper's P
Lateral	1 - 11	2 and 3	decreasing	-.93	<.001	<.001
Dorsal	1 - 7	2	increasing	+.94	<.01	<.001
	8 - 11	3	decreasing	-.90	<.05	.01
Anterior	1 - 7	2	increasing	+.31	>.10	.30
	1 - 11	2 and 3	increasing	+.86	<.005	<.001
	8 - 11	3	increasing	+.80	.05	.01

and heliotaxis, and animal locations in webs or retreats. We resist, however, while our experiments continue, and confine ourselves to some critical comments about the present data.

Is it not possible that the attitudes and changes reported here are not geotactic, and are neither genetic nor adaptive: that they reflect reactions to other environmental conditions such as conformation of thread in the tangle, or space available among siblings, or the direction of incident light in the laboratory? *Mallos gregalis* (Simon), a social spider, adopts attitudes in the laboratory that seem to conform to thread arrangement, which in turn reflects the shape of their container (Kimmel, unpubl. observations). The cage top was flat and horizontal in our experiments on *Nephila*. Although the communal web was a three dimensional structure, its major axis was also horizontal. Second instar spiderlings usually hang suspended by their legs. A second instar animal on horizontal threads is apt to hang in dorsal attitude. Some third instar spiderlings remain on the periphery of the group when they return to it after molting, where they may be relatively free to adopt the anterior attitude. Although it appeared that third instars took the anterior attitude regardless of their location in the tangle, no data on location were kept and instances of other attitudes were noted.

Aside from whether the attitude change is imposed by conditions external to the spiderling in the laboratory other than gravity, we wonder about whether it is a discrete change, occurring abruptly after the second molt. No attempt was made to distinguish individual spiderlings in the group; we show changes in attitudes in a population. Any argument about adoption of the anterior attitude being prerequisite for dispersion, orb building, etc., should be buttressed with a description of the variation of attitudes, if any, in which individual animals rest, over time, before they disperse. There is evidence that dispersion is not a sudden, all-or-none event: in the laboratory it seems to begin as a tendency for spiderlings to spread out gradually in the communal web (Burch 1979). Dispersion appears to continue as migratory cycles in *Nephila*, some individuals returning to the group even after having constructed distant geometric webs (Kimmel and Grant, unpubl. data). The attitude change as well might not be discrete, and thus perhaps not initiate the set of behavior changes associated with dispersion.

Finally, observations were made in the laboratory, in artificial confinement, and upon variable numbers of individuals from a single egg sac. Several experiments will be carried out, in the field and in the laboratory, to approach answers to these problems.

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PRESENCIA DE LA FAMILIA DAESIIDAE EN AMÉRICA DEL SUR CON LA DESCRIPCIÓN DE UN NUEVO GÉNERO (SOLIFUGAE)

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ABSTRACT

In this work *Syndaesia mastix*, new genus and new species of solifugid from Argentina is described and placed in the family Daesiidae. The synonymy of Amacataidae Muma 1971 = Daesiidae Roewer 1934 is proposed. The family Daesiidae, known so far in Africa, Spain and the Near East is recorded here for the first time in South America, with the following genera for this region: *Amacata* Muma 1971 and *Syndaesia*, new genus. The more important similarities between the males of these two genera consist in the presence in both of a tubular flagellum, traversed by a duct and with an opening at each extremity, and also in the structure of the movable cheliceral finger. The principal differences concern the general shape of the flagellum; the structure of the fixed cheliceral finger and the tarsal segmentation and spine-like armature. Except for these two last characters, females of both genera are very similar.

RESUMEN

En este trabajo se describe un nuevo género y especie de solífugo de la Argentina: *Syndaesia mastix*, al cual se ubica en la familia Daesiidae. Se propone la sinonimia Amacataidae Muma 1971 = Daesiidae Roewer 1934. La familia Daesiidae, conocida hasta el momento en Africa, España y Cercano Oriente, es citada aquí por primera vez para América del Sur, con los siguientes géneros para esta región: *Amacata* Muma 1971 y *Syndaesia*, género nuevo. Las similitudes más importantes entre los machos de estos dos géneros consisten en la presencia en ambos de un flagelo tubular, atravesado por un conducto y con una embocadura en cada extremidad, y también en la estructura del dedo móvil de los quelíceros. Las diferencias principales corresponden a la forma general del flagelo; a la estructura del dedo fijo de los quelíceros y a la segmentación y espinulación tarsales. Excepto por estos dos últimos caracteres, las hembras de ambos géneros son muy similares.

INTRODUCCION

El hallazgo de los solífugos que motivan la realización de este trabajo me ha sugerido la necesidad de replantear la validez y las interrelaciones existentes entre algunas familias de solífugos, principalmente Ammotrechidae, Daesiidae y Amacataidae.

Las dos primeras familias mencionadas fueron creadas por Roewer (1934) y son producto de la división que este mismo autor efectuó de la subfamilia Daesiinae Kraepelin 1899 (ubicada en ese momento en la familia Solpugidae). En la clave que Roewer (op. cit.: 262) organiza para las familias de solífugos, da los siguientes caracteres para diferenciarlas: a) flagelo del macho inmóvil (Ammotrechidae) o con una movilidad de 180° alrededor de su eje (Daesiidae) y b) presencia ocasional (Ammotrechidae) o ausencia (Daesiidae) de un diente parietal interno en el dedo móvil de los quelíceros. En las diagnósisis respectivas a ambas familias Roewer agrega otros caracteres diferenciales como son, en algunos géneros de Daesiidae, la presencia de ctenidios en los esternitos o de setas modificadas que acompañan al flagelo. Pero tanto a éstos como el de diente parietal interno en el dedo móvil de los quelíceros (en algunos Ammotrechidae) no puede considerárselos caracteres definitorios de familia, ya que no siempre se presentan. Por otra parte, he observado en algunos Ammotrechidae sudamericanos la presencia de ctenidios (dato inédito). Por lo que conozco, tampoco hay diferencias substanciales en prosoma, patas o pedipalpos. Con esto quisiera hacer resaltar que Ammotrechidae y Daesiidae son dos familias de solífugos estrechamente emparentadas, y que el único carácter importante para poder separarlas reside en la movilidad o no del flagelo del macho. Un hecho interesante es notar que la forma de fijación del flagelo al quelícero relaciona ambas familias. En Ammotrechidae (excepto en los Mummuciinae, cuya elevación a rango familiar sería tal vez necesaria) el flagelo se adosa firmemente al quelícero por medio de un fuerte anillo de fijación, de forma ligeramente ovalada y que no le permite el menor movimiento. El flagelo en si está constituido por una delicada lámina ovalada, más o menos alargada en sentido longitudinal y con los bordes dorsal, ventral y posterior ligeramente curvados hacia el plano medio, lo que lo asemeja a una pequeñísima cuchara (en Mummuciinae es una vesícula con una estrecha abertura en el ápice). El flagelo presenta sus bordes libres, especialmente hacia la mitad apical, ornados de diminutas espículas (Fig. 15), cuya importancia comentaré más adelante. En todos los Ammotrechidae el extremo delgado del flagelo está dirigido hacia adelante. En los Daesiidae el flagelo también está sujeto al quelícero por medio de un anillo de fijación, pero puede rotar paraxialmente sobre él en un ángulo de hasta 180° . En esta familia el flagelo en estado de "reposo" se presenta con el extremo más agudo dirigido hacia atrás, pero el solífugo es capaz de dirigirlo hacia adelante por efectos de algún mecanismo especial, quizás presión hidrostática. Es de hacer notar que este tipo de unión del flagelo al quelícero por medio de un anillo de fijación y sin otras estructuras asociadas es exclusivo de estas dos familias, y que en los otros solífugos que tienen flagelo móvil: Ceromidae, Hexisopodidae y especialmente Galeodidae, se presentan algunas diferencias que veremos más adelante. Otro carácter que relaciona Ammotrechidae con Daesiidae es la semejante segmentación de los tarsos II, III y IV, y que fuera utilizado por Roewer en sendas divisiones subfamiliares.

La otra familia de solífugos que deseo mencionar es Amacataidae Muma 1971, que comprende hasta el momento un solo género y especie de Chile: *Amacata penai* Muma 1971. Luego de efectuar la diagnósisis de la familia Muma expresa: "Male specimens of this family run through the keys in Roewer (1934) to the couplet just before that separating the families Ammotrechidae and Daesiidae. They are readily distinguished from ammotrechids by the complex movable male cheliceral flagellum. The distinctive flagellum, the unusual tarsal segmentation and the spinelike setal armature of the tarsi also distinguishes them from daesiids." Es indudable que el complejo flagelo móvil de *Amacata* permit distinguirlo de cualquier Ammotrechidae, pero respecto a las supuestas diferencias con los

Daesiidae, hago notar que el flagelo no es muy diferente al que presentan varios representantes de esa familia (la más variada en cuanto a morfología de esta estructura); que la segmentación tarsal (1/2/2/4) es idéntica a la que presenta, por ejemplo, la subfamilia Daesiinae y que la correspondiente espinulación tarsal podría entrar perfectamente en esta última subfamilia (Roewer, op. cit.: 388). Ningún otro carácter de los atribuidos por Muma a Amacataidae permite distinguirlo de los Daesiidae, por lo que propongo la sinonimia Amacataidae Muma 1971 = Daesiidae Roewer 1934. Al parecer Muma no estaba muy seguro ni de la validez de su familia Amacataidae ni de la exacta ubicación sistemática de *Amacata*, ya que en un trabajo posterior (Muma 1976: 10) expresa: "*Amacata* Muma from Chile may also belong to the Ceromidae but for the present is maintained in its monotypic family (Amacataidae) because of differences in leg 1 tarsal claws, leg tarsal segmentation and geographical dislocation."

En todo lo expuesto he deseado hacer resaltar que la movilidad y secundariamente la estructura del flagelo son dos de los caracteres más importantes en la diferenciación familiar en Solifugae, hecho, por otra parte, ya admitido por revisores como Roewer (op. cit.) y Muma (1976).

En el presente trabajo se describe un nuevo solífugo de la Argentina, que denomino *Syndaesia mastix* género nuevo y especie nueva y al cual ubico en la familia Daesiidae. La inclusión de este nuevo género en cualquiera de las otras familias que poseen flagelo móvil la he desechado por las siguientes razones: en Galeodidae, por la ausencia de uñas tarsales pilosas y por la diferente inserción del flagelo, ya que aquí lo hace en el centro de una depresión circular y posee, al parecer, una movilidad algo más limitada que en las otras familias; en Ceromidae, por la ausencia de postarso y de 2 uñas en la pata I y por la estructura del flagelo, el cual tiene además una serie de setas asociadas (observado en *Ceroma* sp.) muy particulares; y finalmente en Hexisopodidae por una gran cantidad de caracteres, entre los que se puede mencionar los tarsos II y III modificados para la excavación; la inserción del flagelo es semejante a Ceromidae.

La inclusión de *Syndaesia* en la familia Daesiidae me parece aceptable, aunque indudablemente, como lo reconocen varios autores: Delle Cave y Simonetta (1971) y Muma (1976), el nivel subfamiliar y genérico establecidos por Roewer en esta familia deberá ser revisado a la luz de los nuevos conceptos sobre la validez de ciertos caracteres. Es por esta razón que no ubico a *Syndaesia* en ninguna de las subfamilias conocidas de Daesiidae hasta que este problema sea resuelto.

Indudablemente, un inconveniente se presenta en poder distinguir a las hembras de Ammotrechidae de las de Daesiidae, ya que la ausencia del flagelo en este sexo priva al investigador del carácter más importantes (casi se podría decir el único) para diferenciarlas. La segmentación y espinulación tarsal tal vez puedan ser de cierta ayuda una vez que hayan sido convenientemente valoradas. Por lo tanto, es muy posible que alguno de los géneros sudamericanos de Ammotrechidae descriptos exclusivamente sobre hembras (vgr. *Chinchippus*) pertenezcan en realidad a la familia Daesiidae.

Syndaesia, género nuevo

Diagnosis.—Daesiidae con los tarsos II, III y IV unisegmentados. Espinulación de los tarsos II y III: 2.2.2.6; espinulación del tarso IV: 2.2.2.2.6. Dedo móvil del quelícero del macho con un diente parietal externo. Pedipalpos del macho sin espinas lateroventrales, pero pueden estar presentes en la hembra. Esternitos sin ctenidios. Coxas de las patas I a

III con gruesas setas terminadas en fúrcula. Hembra con 3 dientes anteriores en el dedo fijo de los quelíceros. Flagelo del macho tubular, con un conducto en su interior; no hay setas especiales asociadas al flagelo.

Especie tipo.—*Syndaesia mastix*, especie nueva.

Syndaesia mastix, especie nueva

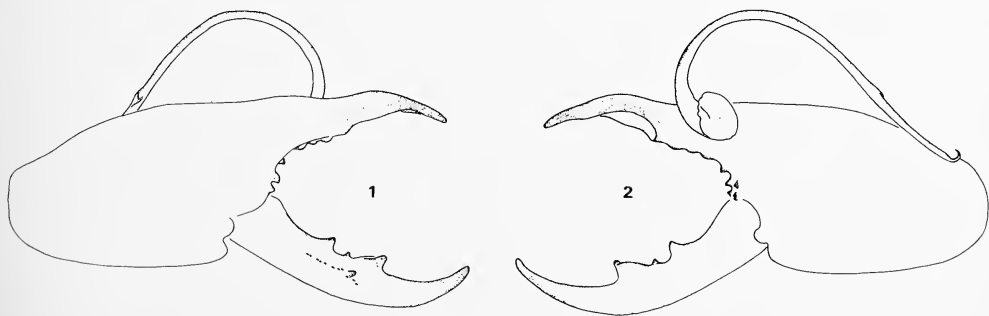
Descripción del Holotypus macho. Medidas en milímetros: Tabla I.

Prosoma. Propeltidio algo más ancho que largo (índice largo/ancho: 0,76). Lóbulos laterales pequeños, poco prominentes, separados por un surco dorsal del propeltidio pero soldados a él posteriormente. Tubérculo ocular con los ojos separados poco menos de 1 diámetro. Todo el propeltidio cubierto de cortas setas; hay otras dispersas, mucho más largas y fuertes. Peltidio en forma de U, con una hilera de robustas setas. Parapeltidio como dos delgadas plaquitas divergentes hacia atrás y afuera, ornadas de pequeñas setas. Mesopeltidio semilunar, bordes laterales y posterior con fuertes setas. Metapeltidio cuadrangular, con largos pelos sedosos y una pocas setas más robustas dispersas. Tergitos cubiertos de largos pelos sedosos, especialmente los 5 primeros, y algunas setas terminadas en fúrcula. Esternitos cubiertos de setas terminadas en fúrcula. Maléolos de pedúnculo relativamente corto; placa siempre más ancha que larga. Coxas de las patas I a III con algunas setas terminadas en fúrcula mucho más gruesas que las restantes (Fig. 13). Quelíceros. Dedo móvil con el mucrón largo, curvado y puntiagudo; sin cresta dorsal. Dentición: hay 4 dientes, 1 diente anterior que es el mayor de todos y el cual posee una saliencia medial (Fig. 5) que semeja otro diente paralelo, separados por un suave surco; 1 diente intermedio pequeño; 1 diente principal algo más chico que el anterior y 1 diente parietal externo pequeño, romo, ubicado a la altura de la base del diente anterior. Este diente es en realidad el más voluminoso de una serie longitudinal de granulitos que se encuentra en la cara externa del dedo móvil (Fig. 1). Dedo fijo de borde dorsal suavemente ondulado, hay una leve depresión a la altura del nacimiento del mucrón. Mucrón ligeramente arqueado, termina en una punta bien aguda; visto desde sus caras interna y ventral se nota una amplia concavidad (Figs. 2, 6). Dentición: salvo a los basales, es difícil nominar los restantes dientes, ya que se encuentran muy reducidos y modificados. A continuación del mucrón se ve una serie de 3 ó 4 dientes mamilares de tamaño similar, que podrían corresponder a los dientes anteriores (o tal vez a 2 dientes anteriores, 1 intermedio y 1 principal); luego un diente pequeño y más puntiagudo, que podría ser el principal (o el 1º basal externo); 2 dientes basales externos de tamaño similar y 3 dientes

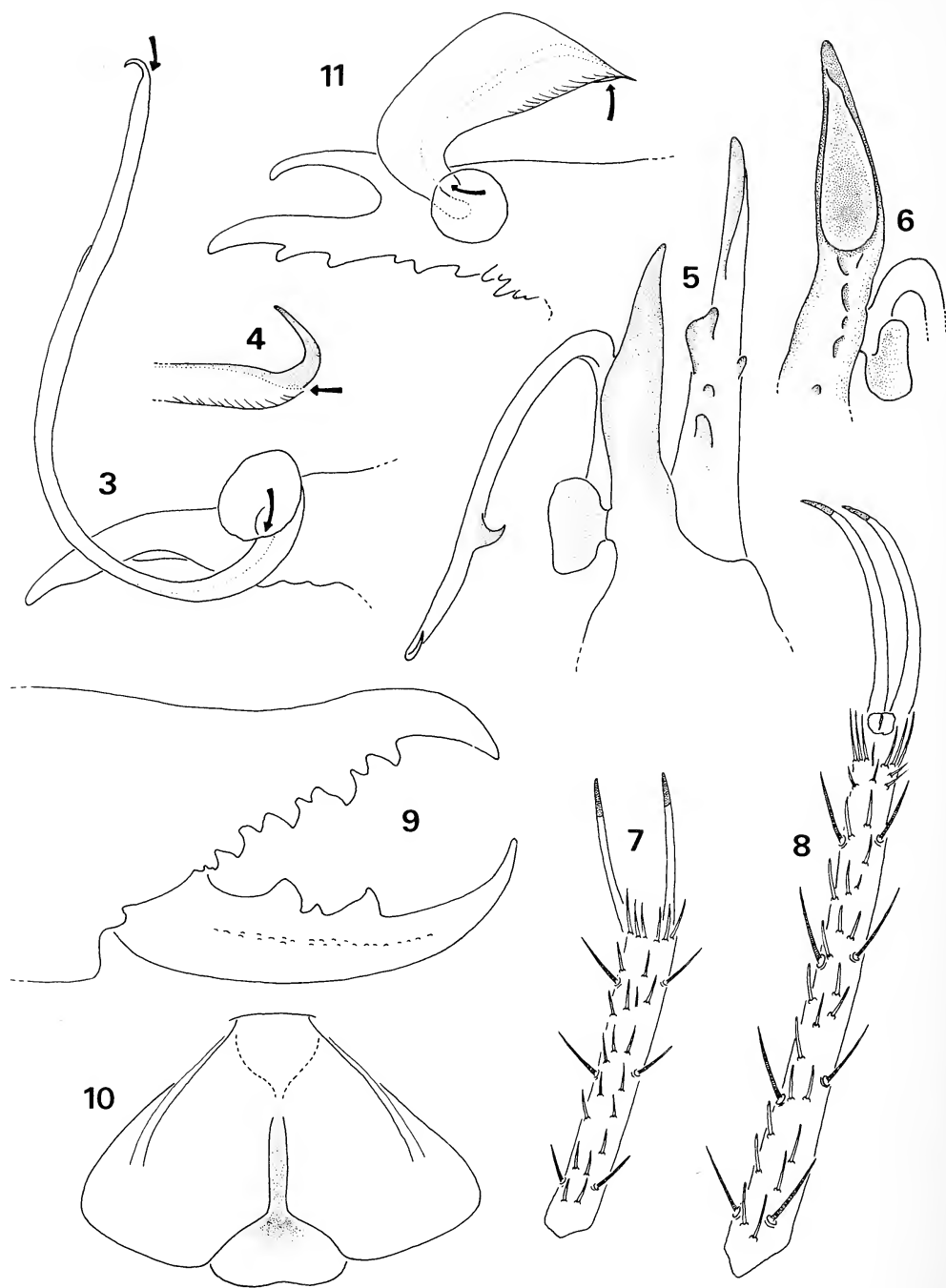
Tabla 1.—Medidas en milímetros de *Syndaesia mastix*.

	Holotypus macho	Paratypus macho
Longitud total	18,69	18,43
Quelícero: longitud	4,16	3,97
ancho	1,28	1,15
alto	1,47	1,34
Propeltidio: longitud	2,43	1,98
ancho	3,20	2,69
Pedipalpo, longitud	14,98	10,56
Pata I, longitud	12,74	11,26
Pata IV, longitud	19,71	16,26

basales internos, el 1^o separado de los restantes por una diastema, el 2^o y 3^o muy pequeños y de base común. El flagelo se encuentra adosado al quelícero por medio de un anillo de fijación sobre el cual puede rotar paraxialmente unos 180^o (la figura 2 muestra al flagelo en estado de “reposo”; la figura 3 erguido unos 90^o). El anillo de fijación se halla situado a la altura del 2^o diente mamilar. El flagelo consiste en una pequeña semiesfera hueca de uno de cuyos bordes se desprende una delgada prolongación en forma de látigo que luego de una amplia curvatura finaliza enangostándose y curvándose bruscamente hacia arriba y afuera, como si fuera un anzuelo. Salvo en el nacimiento y en el extremo distal curvado esta prolongación tiene un grosor similar (aproximadamente 0,12 mm) en todo su recorrido. En la cara externa de la prolongación, aproximadamente a la altura del 1/3 distal, se ve una prominente apófisis triangular quitinizada y curvada hacia afuera y adelante (Figs. 1, 5). Por transparencia se nota que el flagelo está recorrido en toda su extensión por un conducto el que, salvo en la zona próxima a la embocadura distal, ocupa casi todo el espesor. Este conducto tiene 2 embocaduras: la proximal, situada en el interior de la semiesfera adosada al quelícero y la distal, que se abre antes de la curvatura en forma de anzuelo (Figs. 3, 4). Pedipalpos: protarso y tibia con largas setas pero sin espinas lateroventrales. Espinulación patas: pata III: tibia con 2 espinas terminales ventrales y 1 terminal dorsal; protarso con 3 (1.1.1) espinas dorsales y 6 (2.2.2) ventrales. Pata IV: tibia con 2 espinas terminales ventrales; protarso con 4 (1.1.2) ventrales. Espinulación de los tarsos II y III: 2.2.2.6; del tarso IV: 2.2.2.2.6. Esta notación de la espinulación tarsal merece una aclaración. Observada al Microscopio Electrónico de Barrido (MEB), la cara ventral de los tarsos II a IV de *Syndaesia mastix* permite distinguir por lo menos 3 clases distintas de faneras: espinas de “tipo A”, que son rectas (excepto el extremo distal que es algo curvo), lisas, de cuello delgado, ubicadas de a pares en los bordes lateroinferiores del tarso y que se insertan en amplias depresiones crateriformes (Fig. 12 A); espinas de “tipo B”, algo más pequeñas que las anteriores, de superficie ligeramente granulosa, curvadas hacia distal, ubicadas en la cara inferior del tarso aproximadamente en dos filas longitudinales y que se insertan en pequeñas cúpulas sobreelevadas (Fig. 12 B) y pelos largos de “tipo C”, con pequeñas espículas en la superficie, terminados en fúrcula y distribuidos por todo el segmento, principalmente en las caras dorsal y laterales (Fig. 12 C). Estos últimos pelos no tienen importancia en la discusión que sigue, por lo que no volverán a ser mencionados. En las figuras 7 y 8 he tratado de representar esquemáticamente la distribución de las espinas de los tipos A y B en los tarsos III y IV. Es indudable que la notación de la espinulación debería hacerse



Figs. 1-2.—*Syndaesia mastix*, holotypus macho: 1, quelícero derecho, vista externa; 2, quelícero derecho, vista interna.



Figs. 3-8.—*Syndaesia mastix*, Holotypus macho: 3, quelícero derecho, vista interna del dedo fijo y del flagelo (las flechas indican posición de las embocaduras); 4, detalle del apex del flagelo (la flecha indica posición de la embocadura distal); 5, quelícero derecho, vista dorsal de los dedos; 6, quelícero derecho, vista ventral del dedo fijo; 7, tarso III derecho, vista ventral; 8, tarso IV derecho, vista ventral.

Figs. 9-10.—*Syndaesia* sp., hembra: 9, quelícero derecho, vista externa; 10, opérculo genital.

Fig. 11.—*Amacata penai* Muma, Holotypus macho: quelícero derecho, vista interna del dedo fijo y del flagelo (las flechas indican posición de las embocaduras).

exclusivamente sobre un solo tipo de espinas, y lo que parece más lógico es elegir para esto las espinas de tipo A, ya que son las más conspicuas, constantes y las que, por otra parte, fueron utilizadas por Roewer e investigadores posteriores en la sistemática de Solifugae. Pero en *Syndaesia* las 6 espinas terminales de los tarsos II, III y IV pertenecen al tipo B, lo que plantea un problema de difícil solución, ya que son algo más largas que las restantes y su diferenciación de las espinas de tipo A sólo es posible al MEB. Aunque lo más exacto sería, por ejemplo, establecer que la espinulación (basada exclusivamente en espinas de tipo A) del tarso IV de *Syndaesia* es 2.2.2.2.0, esto podría dar lugar a suponer que en distal de ese tarso no hay ninguna clase de espinas, lo cual no es cierto. Por lo tanto he decidido adoptar un temperamento en cierta forma “híbrido” y establecer la notación 2.2.2.2.6, lo cual me parece más sensato y fácil de interpretar si utilizamos una óptica corriente.

Especímenes estudiados.—Argentina: Mendoza; Cerro Divisadero, 15 Km al oeste de Mendoza capital, agosto de 1976 (A. Roig Alsina), Holotypus macho (MACN 7161); Uspallata, Tambillos, 17 de mayo de 1978 (A. Roig Alsina), Paratypus macho (MACN 7165).

Las hembras en el género *Syndaesia*.—He identificado 4 especímenes hembras como pertenecientes al género *Syndaesia*. La peculiar espinulación de los tarsos y las gruesas setas terminadas en fúrcula de las coxas I a III permite distinguirlas de las hembras de *Amacata* o de las de cualquier Ammotrechidae conocido. Es bien sabida la dificultad que se presenta al investigador para atribuir las hembras de los solífugos a los machos coespecíficos. Como *Syndaesia* no es una excepción en este aspecto, he considerado más prudente determinar a estos 4 ejemplares meramente como *Syndaesia* sp., máxime que algunas diferencias morfológicas observadas podrían corresponder a especies distintas. Las figuras 9 y 10 corresponden al ejemplar proveniente de Mendoza. Los quelíceros y el opérculo genital son similares en los 4 especímenes estudiados, pero noté diferencias en la espinulación de los pedipalpos, ya que hay 3 ejemplares con fuertes espinas y 1 (el de Mendoza) en el cual son muy débiles y están en menor número. El tamaño observado varió entre 2,0 y 2,5 cm. Las hembras de *Syndaesia* sp. estudiadas tienen la siguiente procedencia: Argentina: Mendoza, Cerro La Gloria, septiembre de 1976 (A. Roig Alsina), 1 ejemplar (MACN 7166); Rio Negro, General Roca, octubre de 1963 (A. Bachmann), 1 ejemplar (MACN 7162); agosto de 1963 (A. Bachmann), 1 ejemplar (MACN 7163); Chile: Valparaíso, Cerro La Campana, 27 de agosto de 1967 (C. Villagrán), 1 ejemplar (MACN 7164).

Relaciones entre *Syndaesia*, *Amacata* y algunos otros géneros de Daesiidae.—Aparte de *Syndaesia mastix* he estudiado los tipos de *Amacata penai* y especímenes de *Biton striata* (Lawrence 1928), *Blossiola crepidulifera* Purcell 1902, *Gluvia dorsalis* Latreille 1817 y *Tarabulida* sp. Entre las dos primeras especies mencionadas son los quelíceros del macho las estructuras que brindan más útiles elementos de comparación. Como ya expliqué, la dentición del dedo fijo de *Syndaesia mastix* es muy difícil de establecer, ya que los dientes están reducidos en tamaño y muy modificados. Pero es interesante establecer una comparación entre el respectivo dedo móvil. Por primera vez en solífugos sudamericanos se menciona para *Syndaesia* la presencia de un diente parietal externo, el que en realidad es uno de los gránulos de una serie longitudinal que ha experimentado un considerable desarrollo. Tanto en el Holotypus como en el Paratypus macho de *S. mastix*, y en ambos quelíceros, este diente existe y resalta notablemente. En *Amacata* está presente también dicha serie longitudinal de granulaciones, pero no hay un gránulo que se destaque del resto. Según Muma (1971) *Amacata* posee un “rounded toothlike process mesad of

anterior tooth”, el cual también existe en *Syndaesia*, aunque yo lo considero en realidad como una bifurcación del diente anterior, lo que es bien visible en la figura 5. El flagelo del macho de *Amacata* es, según Muma: “a movable translucent parchment-like two part structure, composed of a small, basal, circular, fringed cup, and a large elongated U-shaped crest. . .”. Pero un dato interesante, y que Muma no menciona, es que todo el flagelo está recorrido interiormente por un conducto, cuyos extremos se abren respectivamente en la “fringed cup” y en distal. En la figura 11 he señalado las correspondientes embocaduras de dicho conducto. *Syndaesia*, tal como lo he descrito, también posee un flagelo recorrido en toda su extensión por un conducto, y las embocaduras están situadas en una forma similar a las de *Amacata* (Fig. 3).

Ya he mencionado que en los Ammotrechidae los bordes libres del flagelo se encuentran ornados de diminutas espículas (Fig. 15). En muchos casos, especialmente en el extremo distal, estos bordes contactan y las espículas, al entrecruzarse con las del lado opuesto, forman un esbozo de conducto. Este esbozo es mucho más notable en varias especies de Daesiidae (vgr. *Biton striata*), en donde los bordes superior e inferior del flagelo contactan en casi toda su extensión. Pero en otras, por ejemplo en *Tarabulida* sp.,

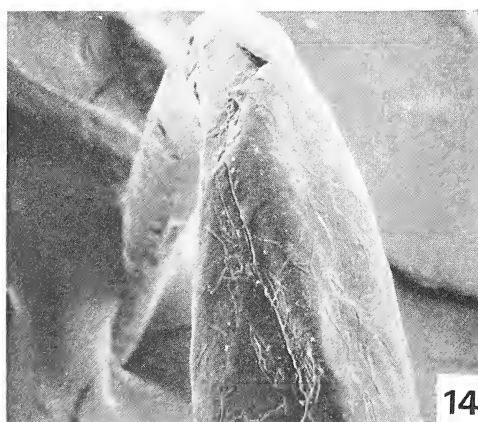
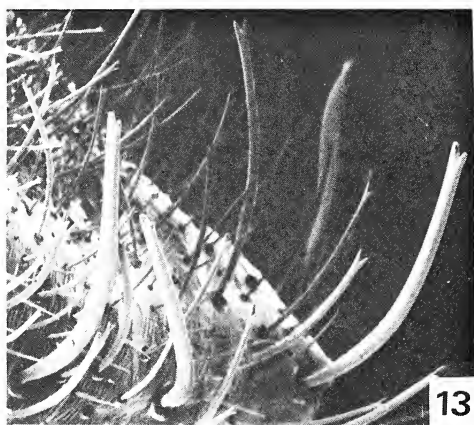
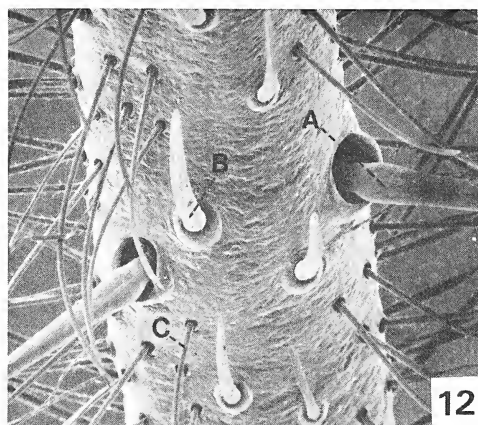


Fig. 12-14.—*Syndaesia mastix*, Paratypus macho: 12, tarso IV derecho, vista ventral (detalle X 300); 13, coxa III derecha (detalle X 150); 14, extremo distal del flagelo (X 1.000).

Fig. 15.—*Procleobis patagonicus* (Holmberg), borde libre del flagelo (detalle X 500).

los bordes libres del flagelo no se tocan, semejándose a muchos Ammotrechidae. Lamoral (1975:139) ha mencionado que en la familia Solpugidae el flagelo posee una costura longitudinal ("seam line"), visible como una serie de pequeñísimos pliegues, y que puede considerarse como el último vestigio de unión entre los bordes libres del flagelo (por soldadura de las espículas se podría añadir). Dicha costura longitudinal es también visible en *Syndaesia* y en *Amacata*, en el borde inferior del flagelo y sobre todo hacia distal (Figs. 4, 11). Todo lo relatado quizás quiera significar que el flagelo "abierto" es una forma primitiva, mientras que el flagelo "cerrado", es decir con conducto, correspondería a formas más evolucionadas. La función que cumple este conducto es aún misteriosa, aunque Lamoral sugiere que podría officiar como conductor y emisor de una feromona sexual.

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REPORT ON A FOSSIL PALPIGRADE FROM THE TERTIARY OF ARIZONA, AND A REVIEW OF THE MORPHOLOGY AND SYSTEMATICS OF THE ORDER (ARACHNIDA: PALPIGRADIDA)

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ABSTRACT

Described in Part I is *Paleokoenenia mordax*, new genus and species, an interesting eukoeneniid palpigrade from the late Tertiary of Arizona. Part II includes important morphological descriptions of the Palpigradida, some of which are important to inter- and intraordinal relationships. Part III provides a review of the systematics of the supraspecific taxa, the number of species known, and includes diagnoses of and a key to the two families and seven genera. Also given is a list of the species with their general distribution. Part IV contains the primary bibliographic references for the order.

INTRODUCTION

Arachnid fossils have been known from the Bonner Quarry near Ashfork, Arizona since 1944. In that year the San Diego Natural History Museum sent two onyx marble pen bases from that location to Dr. Alexander Petrunkevitch for study. From these pen bases containing two specimens, Petrunkevitch (1945b) described a new fossil schizomid, *Calcitro fisheri*, and erected the family Calcitronidae in the order Schizomida. In that contribution he reports: "In the same pen base with the paratype three other fossils are present, which I refer to the same species. All three are somewhat smaller and poorly preserved. The one which lies about 25mm. from the paratype at a place corresponding to 1 h. on a clock dial is better visible than the other two and shows at the end of the abdomen a three-jointed tail." Also in the same pen base, he reported long appendages belonging to an arthropod he could not identify.

Later, Pierce (1950, 1951) examined other pen bases from the Bonner Quarry and described two fossil schizomids, *Onychothelyphonus bonneri* (family Calcitronidae) and *Calcoschizomus latisternum* (family Schizomidae). There were additional specimens and fragments he could not identify. Pierce (1951) reports: "In addition to all of these specimens are three tiny ones too deep for exact characterization, but unquestionably pedipalps. They may be young. No division of thorax is evident, nor is any cauda."

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As part of an investigation into the schizomids of the New World the senior author examined a number of these pen bases from the Los Angeles County Museum and the San Diego Natural History Museum. Close examination of the smaller forms mentioned above revealed that they were palpigrades. A total of seventeen specimens were found among this material, affording a variety of anatomical views of this palpigrade. In addition to these anatomical studies, it was suggested by Dr. Robert W. Mitchell that a review of the systematics and morphology of the order itself would greatly enhance the value of this contribution. Here presented, then, is the study outlined above, which was updated, revised, and carried through to publication by the junior author.

PART I. A NEW GENUS AND SPECIES OF FOSSIL PALPIGRADIDA FROM THE TERTIARY OF ARIZONA

Paleokoenenia, new genus

Description.—Prosoma: Carapace with distinct anterodorsal cone projecting somewhat diagonally upward. Opisthosoma: Ninth abdominal segment about equal in width to eleventh segment, about half as wide as eighth segment; pygidium slightly narrowed posteriorly; flagellum longer than opisthosoma, segments long and slender. Pedipalps very long and thin.

Comparisons.—See under species account.

Etymology.—The generic name is taken from the Greek epithet *paleo*, meaning ancient, and *-koenenia*. This name is applied because the sole representative of the genus is a fossil species.

Type species.—The type and only known species of this genus is described as follows:

Paleokoenenia mordax, new species

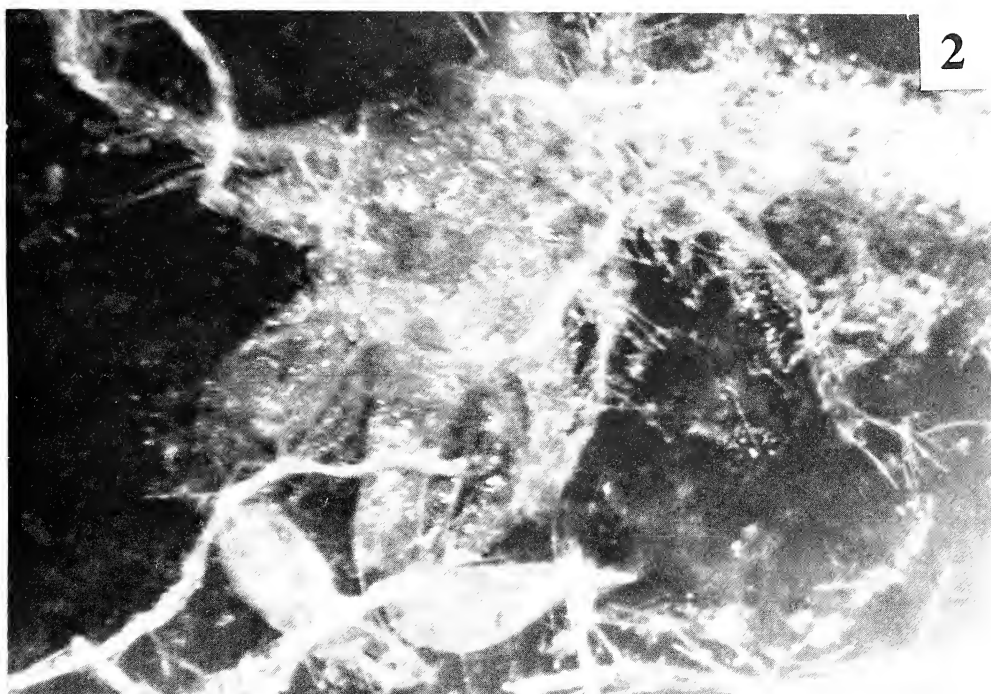
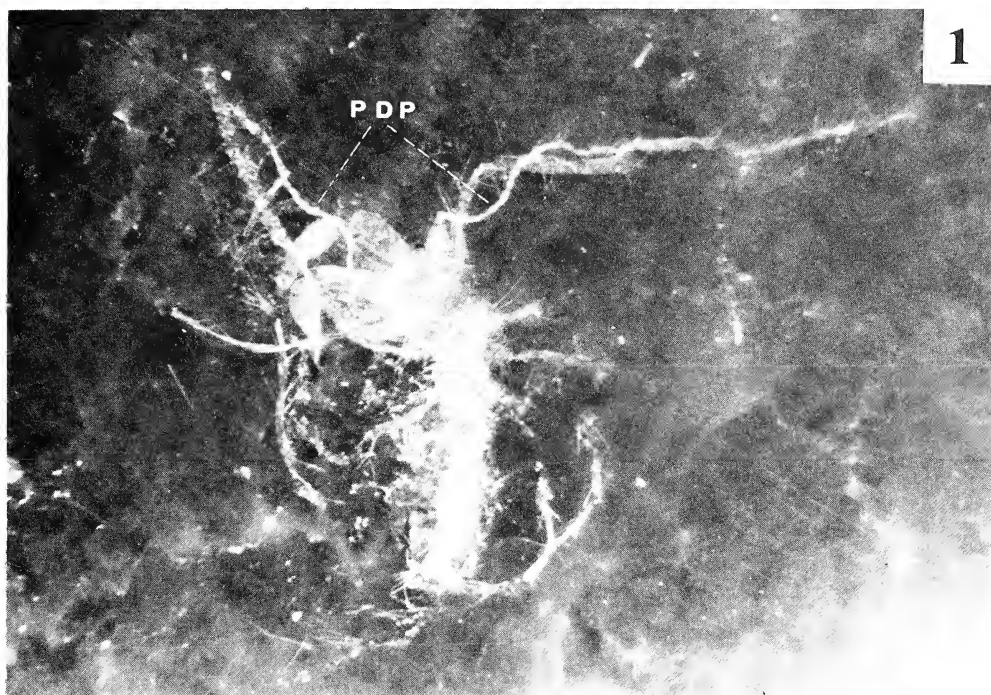
Figs. 1-7

Types.—Holotype (SDSNH Paleo No. 16661), allotype (SDSNH Paleo No. 16662), and fifteen paratypes (SDSNH Paleo Nos. 16663-16677), specimens in calcite pen base mined from Bonner Quarry, 17 mi SW Ashfork, Arizona, NW1/4 of Section 21, Township 20N (southern boundary 35°00'N Lat.), Range 3W (eastern boundary 112°00'W Long.). Altitude 1624 m. Probably Pliocene. Deposited in the Natural History Museum, San Diego Society of Natural History, San Diego, California.

Etymology.—The specific name is taken from the Latin *mordax*, meaning biting, which describes the somewhat formidable chelicerae in this species.

Description.—The following is based on characters selected from wherever possible within the type series. All measurements are in millimeters, and taken from the holotype, except where indicated in parentheses.

Prosoma—Carapace (propeltidium, first prosomal tergum): length 0.54, width 0.23; slightly wider anteriorly than posteriorly, with subapical cone projecting anterodorsally. The anatomy of the ventral surface of the prosoma could not be ascertained, although several coxae of the legs and pedipalps were viewed well enough to enable measurement. The structure of the sterna requires clearing and is difficult to ascertain even in slides of fresh material.



Figs. 1-2.—Dorsal views of the holotype of *Paleokoenenia mordax*, new species: 1, whole view with pedipalps indicated (PDP); 2, close up showing, in particular, the propeltidium and chelicerae.

Opisthosoma—Length 1.5 (allotype), width 0.35 (allotype). Terga with several setae, 0.15 (allotype) in length. Tergal lengths: IV, 0.17; V, 0.16; VI, 0.14; VII, 0.13; VIII, 0.09. Pygidium with several setae in circular arrangement, 0.17 (allotype) in length. Pygidial segment lengths and widths: X, 0.07:0.10; XI, 0.16:0.10 (allotype) with four sets of setae spaced about 0.08 (allotype) in length.

Chelicerae—Length 0.85. Cheliceral segment lengths and widths: basal segment 0.38:0.21 (at widest), second segment 0.46:0.18 (at widest), third segment (movable finger) 0.25 in length. Basal segment tapering distally, with several short and a few longer setae present, second segment with several long and short setae, a particularly strong one on ventral surface 0.06 in length, fixed digit with a curved row of seven teeth along inner margin, third segment with a curved row of several teeth along inner margin, a stout seta 0.11 in length about one fourth the way out on the dorsal surface.

Pedipalps—Length about 1.5, thinner than leg I, several long setae 0.20 in length. Coxal length and width 0.16:0.11.

Legs—I at least as long as pedipalps, but total length not measurable; coxal length and width 0.19:0.08. II, total length not measurable; coxal length and width 0.13:0.13, with several long and short setae, the longest 0.24. III, total length not measurable, coxal length and width 0.14:0.11, with a few long setae, the longest 0.26. IV, no measurements possible.

Flagellum—Total length not measurable, first segment 0.28 in length. Each segment with one or more whorls of setae.

Comparisons.—*Paleokoenenia mordax* differs from all other eukoeneniids in having a pronounced conical protuberance anteromedially on the carapace. The pedipalps are much longer than in any other genera, being about equal in length to the opisthosoma. It seems to be most similar to *Eukoenenia*, *Allokoenenia*, and *Koeneniodes* in morphology of the pygidium, which in all is distinctly narrower than the eighth opisthosomal segment. The accompanying key will separate the genera of palpigrades, of which only *Sternarthron* and *Paleokoenenia* are represented by fossils.

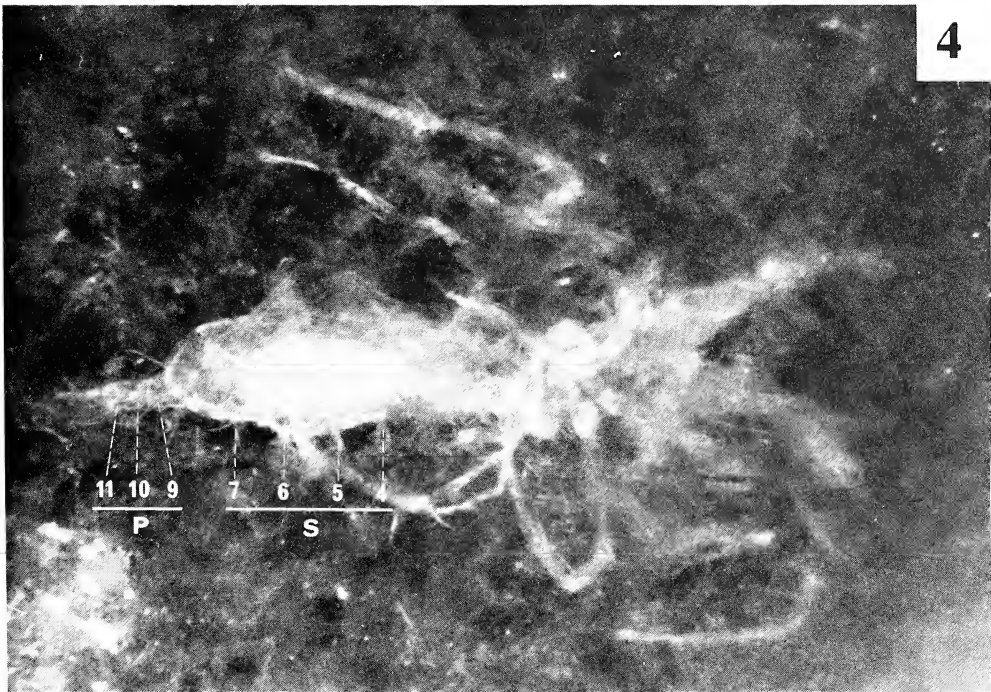
Measurements.—The total length (from anterior margin of prosoma to posterior margin of pygidium) of all measurable specimens 1.7 to 2.4, the holotype and allotype are 1.8 and 2.2, respectively.

Variations.—No variations disproportionate to total length were noticed.

Distribution.—*Paleokoenenia mordax* is known only from onyx deposits at Bonner Quarry, 17 mi SW Ashfork, Arizona.

Age.—The onyx marble containing these specimens was mined from Bonner Quarry by members of the Southwest Onyx and Marble Company from faulted Middle Permian Supai formations on the side of a high angled fault. E. D. McKee was quoted by Petrunkevitch (1945) as stating "The fault passes under and therefore, antedates basalt flows a few miles to the west and these are of a period I consider to be of Pliocene age. The age of the deposit is definitely 'post-faulting' which means since the middle of Cenozoic time, but deposition might have been any time from then to the present." Pierce (1951) gave an age of between 12 and 50 million years. Petrunkevitch (1955) dated other fossils found in this formation as "Pliocene", which for lack of other information, we will follow here.

Natural History.—The nature of the structure of the onyx formation suggests that it was laid down by subterranean waters in fissures. Petrunkevitch (1945) suggested that the animals in the onyx were probably washed into the fissures from epigean habitats and became fossilized. Judging by the frail nature of palpigrades it is difficult to imagine



Figs. 3-4.—Views of *Paleokoenenia mordax*, new species: 3, close up of the dorsal aspect of the abdomen of the holotype with the third through the eighth terga labeled; 4, whole view of the ventral aspect of the allotype with the fourth through the seventh sterna (S) and the ninth through the eleventh abdominal segments or pygidium (P) labeled.

specimens being washed in and remaining in the excellent condition of many of the specimens. It is more probable that these animals lived in close proximity to the area of deposition, which suggests that these palpigrades might have been cavernicoles.

The assemblage of fossils present in the onyx is strongly reminiscent of faunas encountered in moist subtropical caves today. Palpigrades are characteristically found only in moist micro-environments, and their occurrence in temperate areas probably indicates a relictual distribution since more pluvial times. The palpigrades from Bonner Quarry may bear witness to the more humid environment attributed to the late Cenozoic of the southwestern United States. Represented in the onyx are three genera of schizomids, three genera of diplurans, two genera of millipedes and two genera of silverfish. Some of these fossils appear to display troglobite facies, such as attenuated appendages, which make it seem even more likely that these animals were cave dwellers.

Remarks.—The minute, primitive arachnids of the order Palpigradida have been of considerable interest since their discovery in Sicily in 1885. Some 50 species have been described and are placed in five extant and two fossil genera. Two families are recognized, one of which is monotypic, based on the Jurassic *Sternarthron zitteli* Haase, 1890.

The discovery of palpigrades in the middle to late Canozoic of Arizona is of some importance. They are quite similar to members of modern genera, however, and will not create the excitement that *S. zitteli* has. The latter fossil has received much attention since its assignment within the Palpigradida. The material was originally identified as *Halometra minor* Oppenheim, 1887, a primitive water-associated insect. The general appearance and size of *S. zitteli* is, in fact, more suggestive of water striders than other palpigrades. A further examination of these fossils, using modern techniques, is needed to add credence to their assignment within or exclusion from the Palpigradida.

The seventeen remarkably preserved specimens of the species described here attest to the high quality of fossils found in onyx. These fossils are perhaps second in quality only to some amber fossils. This material also reveals something of the past distribution of palpigrades and the climatological conditions which probably prevailed.

No significant results have yet been gathered by various efforts to solve basic questions about the mode of life of palpigrades. They appear to prefer humid micro-environments and occur with great regularity in some localities. They have been collected in humus in caves and under rocks, where moist conditions prevail, but members of *Leptokoenenia* live interstitially. Palpigrades possess formidable chelicerae, but otherwise their frail body does not seem built for a predatory existence. Rucker (1903) suggested that they feed on arthropod eggs, but nothing seems to support this idea. It is likely that they feed on small arthropods such as mites, although no evidence is available.

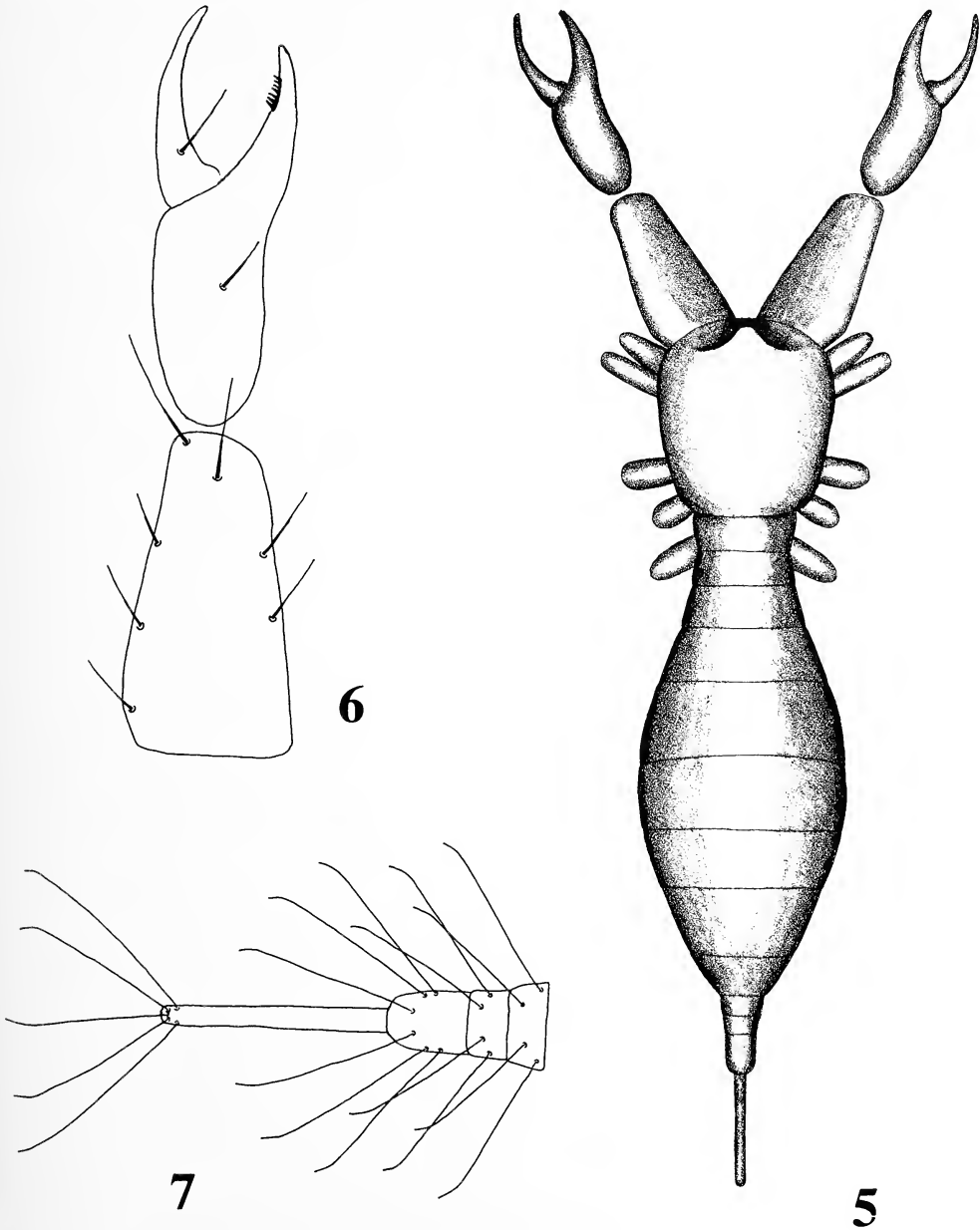
PART II. MORPHOLOGICAL NOTES ON THE PALPIGRADIDA

The following account draws heavily from the works of Börner (1901), Hansen (1901), Hansen and Sörensen (1904), Millot (1943; 1949) Roewer (1934), and Rucker (1901; 1903).

The prosoma is segmented into three components, the propeltidium, mesopeltidia, and metapeltidium. Structures of the same names are found in the Solpugida and Schizomida. Because of the difficulty of obtaining embryological data the interordinal relationship of these structures will be difficult to ascertain, but will be of interest.

The prosoma bears the trophic and locomotor appendages, and special sensory organs, but lacks eyes. It is covered for the most part by the propeltidium, which extends from

above the chelicerae to approximately above the third pair of walking legs. Lateral to the posterior margin of the prosoma are two small plates, the mesopeltidia. These are reported to lie just dorsal to the third pair of walking legs, although they could not be found in preparations of *Eukoenenia hanseni* (Silvestri) and *Prokoenenia wheeleri* (Rucker). Directly above and behind the mesopeltidia is the undivided metapeltidium,



Figs. 5-7.—Reconstructions of *Peleokoenenia mordax*: 5, generalized reconstruction, showing only coxae of pedipalps and legs and first flagellar segment; 6, left chelicera; 7, pygidium and first flagellar segment.

which also lies directly above the fourth pair of legs. Situated at the prolateral and promesal aspects of the propeltidium just above the chelicerae and pedipalps are the relatively robust sensory setae which are discussed further below.

The ventral surface of the prosoma is occupied by eight pedal coxae and the five elements of the sterna. These are of special interest because of their primitive number and character, though they are difficult to observe in all but the best microscopical slide preparations. The largest sternal piece is the fused deuto-tritosternum which lies between the pedipalps and first pair of walking legs. Anterior to this sternal piece is the lower lip of the mouth which is generally considered to be the prosternum. Following the deuto-tritosternum and lying between the second, third, and fourth pair of walking legs are the tetrasternum, pentasternum, and metasternum, respectively.

The first pair of appendages, the chelicerae, are composed of three elements. The basal piece articulates with the second piece which reflects posteriorly and articulates with and opposes the third piece. The tips of the chelae rest just below the opening of the mouth. The inner surfaces of these two pieces each have a single row of seven to ten serrated teeth. As regards the naming of the various appendage articles there are some divergent opinions. According to Van der Hammen (1969) in the chelicerae a basal coxal region is followed by the trochanter, which was considered basal before his work. Following the trochanter is the "principal cheliceral segment" formed by the fusion of femur, patella (genu), tibia, and tarsus. The movable chelal digit is named the apotele.

According to classical works the second pair of appendages, the pedipalps, are composed of nine elements. The patella is absent, and the extra number of segments is due to the subdivision of the basitarsus into two and the tarsus into three pieces. There exist two well developed claws and the appendage serves mainly, as far as is known, in locomotion. Van der Hammen (1969) reported having found evidence of a segment basal to what had previously been considered the coxa. He considered this article to be the true coxa and the coxa of other authors he considered the trochanter. From the work of Snodgrass (1948) we must also consider that a pedipalpal patella is present, which he demonstrated convincingly for spiders and the "pedipalpi". Acceptance of the findings of both Van der Hammen and Snodgrass preserves the nominal designation of segments including and distal to the tibia.

The legs possess, from first to fourth, twelve, seven, seven, and eight elements. The basitarsus of leg I is divided into four pieces and the tarsus into three. The basitarsus and tarsus, as well as the other pieces, are simple in legs II and III. In leg IV the tarsus is two segmented. The first leg is reportedly not ambulatory but, as in the "pedipalpi", functions mainly as a tactile organ. The possession of claws on leg I suggests, however, that the leg may serve at least some locomotory role. On all legs and the pedipalps there is a pretarsus with two lateral and a smaller median, or pseudonycial, claw.

The names and implied serial homologies of the articles of the walking legs have not been the source of much dispute. Certainly the articles proximal to and including the tibia seem to present a fairly clear picture, though Hansen (1931) offered some alternatives to the classical interpretation of articular homologies. Accepted here are Hansen and Sørensen's (1897) interpretation of leg segments. The pedipalp and first walking leg present serious problems in interpreting which of the various subsegments of the appendages distal to the tibia corresponds to the basitarsus (metatarsus) and which corresponds to the tarsus. Hansen and Sørensen (1897) in setting down the interpretation in use today said, "... we deviate somewhat from Grassi. . . with regard to the boundary line between metatarsus and tarsus. However, . . . we cannot insist with absolute certainty

on the correctness of our view, as it is only based on a personal estimate.” The second and third walking legs are represented by the usual arachnid complement of seven articles. The fourth pair have a divided tarsus according to Millot (1949).

The opisthosoma is usually considered to show evidence of only eleven segments rather than the twelve encountered in some orders. Twelve is considered primitive in the Arachnida. The abdominal terga and sterna are not distinguishable as clearly defined units in palpigrades, rather they are marked by a somewhat thicker pubescence than the intervening pleural regions. The anterior and posterior tergal and sternal borders are, by contrast, sharply delineated by clearly visible sutures. Abdominal segments VIII-XI lack a noticeable reduction in pubescence on the lateral borders, hence in these segments perhaps there is no pleura separating terga and sterna.

The genital organs open to the outside behind the second abdominal sternum as in most other arachnids. Several setational modifications on this sternum and the following one comprise external sexually dimorphic characters. In some species there exist three pairs of sacs, one pair each on sterna four, five, and six. They are purportedly eversible as are the ventral sacs of amblypygids. They are called lung-sacs by those who attribute some respiratory function to them, but no evidence exists as to their function.

The eleventh abdominal segment bears the anus and the flagellum. The flagellum is usually composed of 14-15 units. Evidence exists, however, that each pair of these actually forms a single unit.

The basal flagellar element in at least some, and perhaps all palpigrades is markedly different from the following ones. The setational pattern is much different. There are two dorsal and two larger ventral setae on the basal element, whereas there are one or two whorls of setae on the units following. Furthermore, Monniot (1970) reported that the cuticular pubescence of the surface of the basal piece was structurally very similar to the parts of the body anterior to it, more so than to the rest of the flagellum. This suggests that the basal flagellar piece may in reality be the twelfth abdominal segment. While the position of the anus depreciates this theory, the problem is not insurmountable. It is easy to visualize a gradual shift in position from subterminal to ventral to subproximal. Such a shift would place the anus between the eleventh and twelfth segments. With no hope of embryological studies being done in this order within the near future the nature of this theory must remain speculative, but the morphological evidence is strong. If we assume that the presence of 12 abdominal segments is primitive in arachnids then the 11 encountered in palpigrades is a derived condition. Evidence from the dorsoventral musculature indicates that a coalescence of segments has not occurred, at least anterior to the seventh abdominal segment. It is, if information of Börner (1904) and Roewer (1934) is correct, the same in palpigrades, schizomids, uropygids, and amblypygids.

The cuticle in palpigrades is nearly totally covered by a variable pubescence, but this is absent from the prosomal pleural areas and the apical parts of the chelicerae. Scattered setae are present over much of the body and that of the prosomal sterna and abdominal terga and sterna are put to taxonomic use. Seven trichobothria are present on the first pair of legs. Two occur on the first and second basitarsal segments and one occurs on the patella, the fourth basitarsal segment, and the second tarsal segment. Palpigrades lack lyriform organs.

The digestive system opens from the mouth which is formed by the upper lip (labrum) and lower lip (prosternum). The buccal cavity above the mouth is lined with rows of sclerotized projections which probably sieve the food as it enters. The buccal cavity leads to the pharynx which is supplied dorsally with an extensive musculature. Van der

Hammen (1969) treats the mouthparts of palpigrades in considerable detail. The esophagus leads into the midgut. The midgut has intestinal diverticulae. One pair occurs in the prosoma and six in the opisthosoma. The midgut empties into the rectum, and the anus terminates the intestine.

The excretory system is represented by nephrocytes and coxal glands. The coxal gland tubules, according to Börner (1904), originate in the anterior part of the third opisthosomal segment. They follow a twisting path forward into the prosoma and from there to the level of the coxae of the first pair of legs follow a straight path until turning ventrally to their opening on this coxa.

Constitution of the circulatory and respiratory systems is poorly known. Conflicting reports of the development of the heart range from absence (Rucker, 1903) to one with four ostia (Börner, 1901). Millot (1949) reported a weakly developed heart extending from the second to fifth opisthosomal segment.

The nervous system is composed of a supra- and subesophageal ganglionic mass. From the supraesophageal ganglionic mass the tritocerebrum issues a pair of cheliceral nerves. The subesophageal mass, besides giving off the pedipalpal and pedal nerves, leads to an abdominal ganglionic mass composed of three neuromeres. The sense organs are apparently limited mainly to sensory setae and trichobothria. A single bifurcate seta is located anteromedially and one to four are located anterolaterally on each side of the carapace. One may perhaps be tempted to somehow relate these structures with the eyes of other arachnids, owing to their numbers and position. Van der Hammen (1969), however, homologized the structures with the supracoxal setae of mites, though no such supracoxal setae are found above the chelicerae in mites.

Nearly nothing is known about the reproductive habits of palpigrades. Remy (1949) gave good indication that palpigrades produce spermatophores which he believed he found on females of Madagascan species. Rucker (1903) also mentioned structures in males construed to be spermatophores. Juberthie and Juberthie (1963) uncovered morphological evidence which also points to probable existence of spermatophores.

The works of Rucker (1903), Börner (1904), Millot (1949), and Juberthie and Juberthie (1963) represent nearly all of our knowledge of the reproductive system. The testes are paired, elongate structures in the ventrolateral spaces of the third to eighth abdominal segments. The females have two ovaries and two oviducts which converge in the uterus. The studies of Juberthie and Juberthie (1963) show that females probably produce only one or two eggs at a time. They also point out the great disparity in the relative abundance in the sexes in a few species. In *P. wheeleri* the males are slightly more common than the females; in *E. mirabilis* only two males as opposed to 400 to 500 females have been collected; and in *Eukoenenia austriaca* (Hansen) six females and four males are known.

As pointed out by Van der Hammen (1974) postembryonic developmental data are fragmentary for this order. Rucker (1903) gave evidence of four stages of development; however, these data were gathered from collections of preserved animals and not from life history studies of living animals.

The musculature has been described to some extent by Börner (1904). The major prosomal muscles are associated with the chelicerae, these being the dorsal protractor, interior rotator, exterior rotator, inferior retractor, and dorsal retractor. The musculature of the endosternite was also originally described by Börner (1904). A careful work by Millot (1943), however, appears to be more complete. As Firstman (1973) pointed out, there are six sets of muscles originating from the endosternite. Four sets have a pair of dorsal suspensors, five sets have a pair of lateral suspensors, and all six sets have ventral

suspensors. He concluded that these sets correspond to the six pairs of appendages which is unique in the Arachnida, and may be correct in assuming this to be the primitive condition.

The abdominal musculature consists of dorsal longitudinals, lateral longitudinals, ventral longitudinals, obliques, and dorsoventrals. Reports on the disposition of the abdominal dorsoventral muscles are confusing. Rucker (1901), Hansen (1901) and Firstman (1973) reported five pairs, apparently representing those occurring in segments two through six. Börner (1904) and Roewer (1934) also reported the five pairs occurring in segments two through six, but also found one extending from the first abdominal tergite attaching on the dorsal surface of the endosternite. In the Uropygida, Schizomida, and Amblypygida there exists a pair of dorsoventral muscles attaching the first abdominal tergum to the dorsal surface of the endosternite. Börner (1904) and Roewer (1934) indicated that the posteriormost dorsal muscles of the endosternite were the first pair of dorsoventral muscles. This is not indicated by Millot (1943) or Firstman (1973). Börner correctly interpreted the relationship of this pair of muscles in the Schizomida, Uropygida, and Amblypygida. Firstman also reported that the first abdominal dorsoventral muscles attach to the endosternite in uropygids and amblypygids, but he missed this relationship in the schizomids.

Judging by the close relationship of palpigrades to the previous orders, Börner's and Roewer's interpretation that the posterior pair of dorsal muscles arising on the endosternite connect to the first abdominal tergite, is considered to be correct rather than Millot's observations, repeated by Firstman, that this pair is entirely prosomal.

PART III. SYSTEMATICS OF THE PALPIGRADIDA

Diagnoses of the families and genera and synopsis of the species of the order Palpigradida

FAMILY STERNARTHRONIDAE HAASE, 1890

Diagnosis.—Second and third prosomal sterna separate, forming six prosomal sterna in all.

Genus *Sternarthron* Haase, 1890.

Diagnosis.—Same as for the family.

1. *S. zitteli* Haase, 1890. Jurassic of Germany.

FAMILY EUKOENENIIDAE PETRUNKEVITCH, 1955

Diagnosis.—Second and third prosomal sterna fused, forming five prosomal sterna in all.

Genus *Eukoenenia* Börner, 1901.

Diagnosis.—Without ventral sacs on opisthosoma; ninth abdominal segment about twice as wide as eleventh segment, slightly narrower than eighth segment; pygidium narrower posteriorly; flagellum longer than opisthosoma; fourth and sixth opisthosomal sterna each form a protuberance.

2. *E. angolensis* (Remy), 1956. Angola.

3. *E. angusta* (Hansen), 1901. Thailand.

4. *E. ankaratrensis* Remy, 1961. Madagascar.
5. *E. austriaca* (Hansen), 1926. Austria.
6. *E. bara* (Remy), 1950. Madagascar.
7. *E. berlesei* (Silvestri), 1905. Italy.
8. *E. brolemanni* (Hansen), 1926. France.
9. *E. buxtoni* (Berland), 1914. France.
10. *E. chartoni* (Remy), 1950. Madagascar.
11. *E. decepatrix* Remy, 1961. Madagascar.
12. *E. delfini* (Remy), 1950. Madagascar.
13. *E. depilata* Remy, 1961. Madagascar.
14. *E. draco* (Peyerimhoff), 1906. Mallorca.
15. *E. florenciae* (Rucker), 1903. Texas, U.S.A.
16. *E. fossati* Remy, 1961. Madagascar.
17. *E. grassii* (Hansen), 1901. Paraguay.
18. *E. hansenii* (Silvestri), 1913. Mexico.
19. *E. hesperia* (Remy), 1953. Ivory Coast.
20. *E. hispanica* (Peyerimhoff), 1906. Spain.
21. *E. juberthiei* Condé, 1974. Lebanon.
22. *E. lauteli* (Remy), 1950. Madagascar.
23. *E. lawrencei* Remy, 1957. South Africa.
24. *E. machadoi* (Remy), 1950. Angola.
25. *E. meridiana* Remy, 1961. Madagascar.
26. *E. mirabilis* (Grassi and Calandruccio), 1885. Italy.
27. *E. patrizii* (Condé), 1958. Sardinia.
28. *E. pretneri* Condé, 1977. Yugoslavia.
29. *E. pyrenaica* (Hansen), 1926. France.
30. *E. remyi* Condé, 1974. Yugoslavia.
31. *E. roquetti* (Mello-Leitão and Arlé), 1935. Brazil.
32. *E. sakalava* (Remy), 1950. Madagascar.
33. *E. siamensis* (Hansen), 1901. Thailand.
34. *E. spelaea* (Peyerimhoff), 1902. France.
35. *E. strinatii* Condé, 1976. Italy.
36. *E. subangusta* (Silvestri), 1905. Italy.
37. *E. trehai* Remy, 1961. Madagascar.
38. *E. vagvolgyii* (Szalay), 1956. Hungary.

Genus *Prokoenenia* Börner, 1901.

Diagnosis.—With ventral sacs on opisthosoma; ninth abdominal segment about twice as wide as eleventh segment, slightly narrower than eighth segment; pygidium narrowed posteriorly; flagellum longer than opisthosoma.

39. *P. californica* Silvestri, 1913. California (?), U.S.A.
40. *P. chilensis* Hansen, 1901. Chile.
41. *P. millorum* Remy, 1950. Madagascar.
42. *P. wheeleri* (Rucker), 1901. Texas, U.S.A.

Genus *Koeneniodes* Silvestri, 1913.

Diagnosis.—Without ventral sacs on opisthosoma; ninth abdominal segment about twice as wide as eleventh segment, slightly narrower than eighth segment; pygidium narrowed posteriorly; flagellum longer than opisthosoma; fourth and fifth opisthosomal sterna form single protuberance.

- 43. *K. frondiger* Remy, 1950. Madagascar.
- 44. *K. madecassus* Remy, 1950. Madagascar.
- 45. *K. malagasorum* Remy, 1961. Madagascar.
- 46. *K. notabilis* Silvestri, 1913. French Guinea.

Genus *Allokoenenia* Silvestri, 1913.

Diagnosis—Without ventral sacs on opisthosoma; ninth abdominal segment equal in width to eleventh segment, half as wide as eighth segment; pygidium not greatly narrowed posteriorly; flagellum shorter than opisthosoma.

- 47. *A. afra* Silvestri, 1913. French Guinea.

Genus *Leptokoenenia* Condé, 1965.

Diagnosis—Without ventral sacs on opisthosoma; ninth abdominal segment slightly wider than eleventh segment, about equal in width to eighth segment; pygidium slightly narrowed posteriorly; flagellum shorter than opisthosoma.

- 48. *L. gerlachi* Condé, 1965. Farasan Islands, Saudi Arabia.
- 49. *L. scurra* Monniot, 1966. Zaire.

Genus *Paleokoenenia*, Rowland and Sissom, 1980.

Diagnosis—Presence or absence of ventral sacs on opisthosoma not determined; ninth abdominal segment about equal in width to eleventh segment, about half as wide as eighth segment; pygidium slightly narrowed posteriorly; flagellum longer than opisthosoma; pedipalps extremely long; carapace with an anteromedian cone.

- 50. *P. mordax*, Rowland and Sissom, 1980. ? Pliocene of Arizona, U.S.A.

Key to the families and genera of Palpigradida

- 1. Prosoma with six sterna; Mesozoic Sternarthronidae; *Sternarthron*
Prosoma with five sterna; Cenozoic Eukoeniidae 2
- 2. Ninth opisthosomal segment about twice as wide as eleventh segment3
Ninth opisthosomal segment equal to or only slightly wider than eleventh segment . .5
- 3. Fourth,fifth and sixth opisthosomal segments with ventral sacs*Prokoenenia*
All opisthosomal segments without ventral sacs4
- 4. Fourth and fifth opisthosomal sterna joined in a midventral protuberance; seventh
opisthosomal sternum with a pair of long, stout, posteriorly directed setae
.....*Koeleniodes*
Fourth and sixth opisthosomal sterna each forming an independent protuberance;
seventh opisthosomal sternum without a pair of long, stout, posteriorly directed setae
..... *Eukoenenia*
- 5. Ninth opisthosomal segment about half as wide as eighth segment6
Ninth opisthosomal segment only slightly narrower than eighth segment
.....*Leptokoenenia*
- 6. Flagellum longer than opisthosoma; ninth abdominal segment wider than tenth
segment, and tenth segment wider than eleventh segment; flagellar segments long and
slender; Pliocene *Paleokoenenia*
Flagellum shorter than opisthosoma; ninth and eleventh abdominal segments wider
than tenth segment, ninth and eleventh segments about equal in width; flagellar
segments moniliform *Allokoenenia*

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A NEW SPECIES OF *APOCHTHONIUS* WITH PAEDOMORPHIC TENDENCIES (PSEUDOSCORPIONIDA, CHTHONIIDAE)

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ABSTRACT

A new species, *Apochthonius knowltoni*, is described from southwestern Wyoming. It is apparently unique among pseudoscorpions in having some individuals intermediate in sexual characters between tritonymphs and adults.

INTRODUCTION

For many years Prof. George F. Knowlton, of Utah State University, has collected soil animals in the general area of northeastern Utah, southeastern Idaho and southwestern Wyoming. He has sent most of his pseudoscorpion specimens to me for study and for this I am most grateful. Of the five hundred collections of pseudoscorpions received from him, only one has contained members of the genus *Apochthonius*. These have been found to represent an unusual new species and are described below.

Apochthonius knowltoni, new species
Figs. 1-5

Material.—Holotype male (WM 3812.01001) and 5 paratypes (1 female, 1 tritonymph and 3 intermediate between tritonymph and adult) separated from litter of lodgepole pine and fir 10 miles SE of Smoot, Lincoln County, Wyoming, 7 August 1974, by G. F. Knowlton. Types are in the Florida State Collection of Arthropods, Gainesville.

Diagnosis.—An epigeal species of *Apochthonius* generally similar to *A. occidentalis* but larger, carapace length 0.5-0.6 mm; base of coxal spines with well developed anterior spurs; and some individuals intermediate in morphology between tritonymphs and adults.

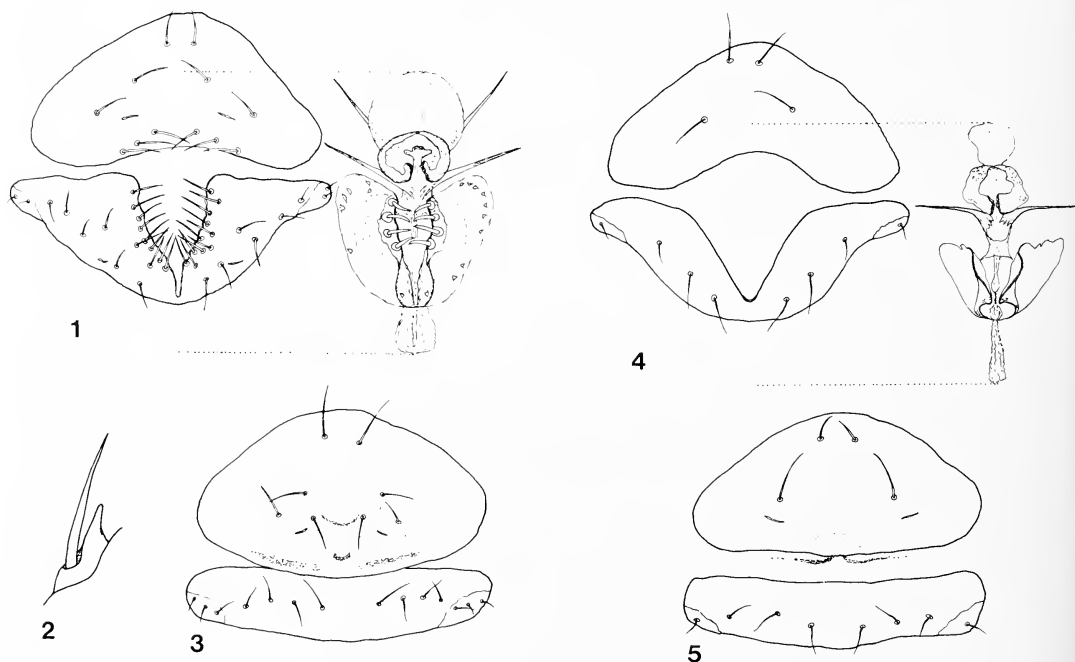
Description of male.—With the general features of the genus (see Muchmore and Benedict 1976). All sclerotized parts light tan. Carapace about as long as broad anteriorly,

narrowed toward posterior margin; with small, dentate epistome; four corneate eyes; chaetotaxy 8-4-4-2-4=22. Abdomen typical of the genus; tergal chaetotaxy 4:4:7:7:9:11:10:11:T2T2T2T:9:1T2T1:0: sternal chaetotaxy 12:[4-4]:(2)10-11/12(2):(3)8(3):mm9mm:m12m:14:16:16:T2T2T2T:0:2; internal genitalia as illustrated (Fig. 1). Coxal chaetotaxy 2-2-1:3-0-CS:2-3:2-3:2-3; each coxa I with three spinelike setae of the usual kind, their bases having well developed anterior spurs (Fig. 2); no intercoxal tubercle.

Chelicera 0.85 as long as carapace; hand with seven setae; flagellum of eight pinnate setae, the most distal one set far apart from the others; each finger with six or seven teeth, decreasing in size basally; no galea evident.

Palp typical; with femur 1.05 and chela 1.55 times as long as carapace; femur 4.85, tibia 2.1, and chela 4.85 times as long as broad; hand 1.65 times as long as deep; movable finger 2.1 times as long as hand. Trichobothria in usual positions. Fixed finger with 65 marginal teeth, all cusped except the basal four; movable finger with 58 teeth, only those in distal half cusped; no teeth conspicuously larger than adjacent ones. Movable finger with rounded sensillum on external surface midway between levels of trichobothria *st* and *sb*.

Legs typical; leg IV with entire femur 2.45 and tibia 4.0 times as long as deep; a long tactile seta on tibia and each tarsal segment of leg IV.



Figs. 1-5.—*Apochthonius knowltoni*, new species: 1, male genital opercula and internal genitalia; 2, a coxal spine showing anterior projection of base; 3, female genital opercula and genitalia; 4, genital opercula and internal genital structures of male intermediate form; 5, genital opercula and internal genital structures of female intermediate form.

Female.—Similar to male but slightly larger and more robust. Chaetotaxy of genital opercula and internal genitalia as illustrated (Fig. 3). Movable finger of chelicera with very low galea. Palp stouter than that of male: femur 4.4, tibia 1.9 and chela 4.5 times as long as broad.

Tritonymph.—Similar to adults but smaller and with reduced numbers of setae on some structures. Carapace with adult number of 22 setae. Tergal chaetotaxy 4:4:6:7:9:9:9:9:-; sternal chaetotaxy 4:(1)6(1):(2)5(2):m7m:m7m:10:11:-. Movable finger of chelicera with a small but distinct galeal elevation. Only two coxal spines on each coxa I. Trichobothria *isb* and *sb* missing from fixed and movable fingers, respectively, as is usual. Fixed finger with 51 and movable finger with 44 marginal teeth; sensillum somewhat proximal to level of *st*.

Intermediate forms.—Similar to tritonymph in most respects, including size and proportions, possession of only two coxal spines on each side, possession of distinct galea, lack of trichobothria *isb* and *sb*, and number of teeth on chelal fingers. Differ from tritonymph and approach adults in development of internal genital apparatus, with distinctly male or female characteristics (Fig. 4 and 5).

Measurements (mm).—Adults (figures given first for holotype male, followed in parentheses by those for female). Body length 1.77(1.83). Carapace length 0.55(0.605). Chelicera 0.465(0.55) by 0.24(0.28). Palpal femur 0.58(0.615) by 0.12(0.14); tibia 0.295(0.30) by 0.14(0.16); chela 0.85(0.895) by 0.175(0.20); hand 0.28(0.31) by 0.17(0.205); movable finger 0.585(0.62) long. Leg IV: entire femur 0.54(0.58) by 0.22(0.235); tibia 0.40(0.42) by 0.10(0.105).

Juveniles (figures given first for tritonymph followed in parentheses by ranges for the three intermediates). Body length 1.47(1.26-1.46). Carapace 0.43(0.41-0.445). Chelicera 0.37(0.355-0.36) long. Palpal femur 0.41(0.38-0.40) by 0.105(0.095); tibia 0.22(0.215-0.22) by 0.12(0.115-0.125); chela 0.60(0.585-0.615) by 0.14(0.13-0.14); hand 0.21(0.19-0.215) by 0.14(0.13); movable finger 0.42(0.39-0.43) long. Leg IV: entire femur 0.37(0.36-0.385) by 0.15(0.15-0.155).

Etymology.—The species is named *knowltoni* in acknowledgement of George F. Knowlton's great contributions to biology in the Great Basin.

Remarks.—The partial development of sexual characters in these otherwise proper tritonymphs is apparently unique among pseudoscorpions although somewhat similar situations are known. Perhaps analogous but carried to the extreme is the condition in *Microbisium* Chamberlin, where mature males (rare) and females are generally tritonymphal in size and morphology (see Nelson, 1975). Also, Benedict and Malcolm (1978) report a somewhat similar situation in *Pseudogarypus bicornis* (Banks), where two specimens with adult genitalia are smaller than normal and have only three trichobothria on the movable chelal finger.

It is, of course, not known how widely spread through the present species are the paedomorphic tendencies. Only future collecting and study can show whether it is general or only a local aberration.

ACKNOWLEDGEMENTS

I am very grateful to George F. Knowlton for collecting and sending the specimens, and to Charlotte H. Alteri for preparing the illustrations.

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RESEARCH NOTES

UNIDENTIFIED OBJECTS

During the course of an ongoing study of the comparative morphology of the female internal genitalia of haplogyne spiders I noticed a group of about fifteen spherical objects within the posterior receptaculum of a scutate Oonopid spider (*Gamasomorpha* sp.) from Singapore.

The spheres are relatively large (20 microns) and translucent and each of them contain four somewhat twisted elongate structures about 25 microns in length (Figs. 1 and 2).



Fig. 1.—The female internal genitalia of *Gamasomorpha* sp. (Family Oonopidae) from Singapore. The dark sclerotic plate extending across the anterior portion of the organ is a muscle attachment plate while the narrower T-shaped structure in front is the anterior secretory organ. The transverse muscle plates mark the level of the external gonopore. The darker mass within the posterior sac is the coagulated mass of secretory fluid which encloses the unidentified spheres. Photographed with transmitted light. Specimen cleared with Lactic Acid.



Fig. 2.—Eleven intact spheres with a number of free rodlike structures presumably from ruptured spheres within the receptaculum. Photographed with Nomarski illumination.

The genitalia of this group of spiders consists of two structures each opening into the bursa copulatrix a short distance within the gonopore. The anterior structure (T-shaped in this species) has associated with it a large secretory gland while the capacious thinwalled posterior sac receives this secretion. The sperm mass after deposition in the bursa by the male disperses throughout this secretory fluid and is stored mainly in the posterior receptaculum. When charged the sperm show up as granules under moderately high magnification. In this specimen no typical spermatozoa were present.

After dismissing first thoughts that here was a new form of spermatogenesis involving giant spermatozoa the question remained - just what are these objects?

The genitalia were originally examined and photographed while cleared in Lactic Acid but subsequently were washed in distilled water and the spheres expressed. Staining was attempted but without success - the strong translucent coat seems impermeable to stain. Considerable pressure was needed to rupture the coat but when achieved the structures within were unfortunately destroyed.

After consultation with workers representing a wide range of biological disciplines it is clear that the consensus of opinion favours a sporozoan infection.

Has anyone else observed this phenomenon in association with the reproductive organs of spiders or other arthropods?

Ray Forster, Otago Museum, Dunedin, New Zealand.

A NEW CAVERNICOLOUS *APOCHTHONIUS* FROM
CALIFORNIA (PSEUDOSCORPIONIDA, CHTHONIIDAE)

Recent collecting by several people in caves of Calaveras County, California, has revealed a relative wealth of cave-adapted forms of pseudoscorpions. One of these, an *Apochthonius*, is described below as a contribution to the better understanding of this widespread genus in the western states.

I am greatly indebted to A. G. Grubbs for sending the specimens and to C. H. Alteri for preparing the illustrations.

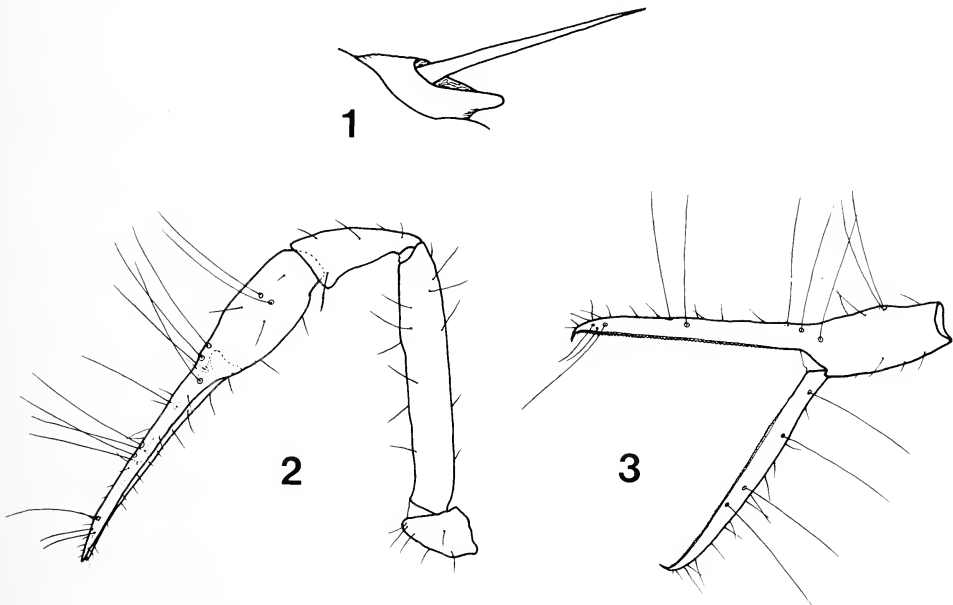
Apochthonius grubbsi, new species

Figs. 1-3

Material.—Holotype male (WM 4749.01001) and paratype female from Music Hall Cave, 4.5 miles SE of Angels Camp, Calaveras County, California, 18 May 1977 (Andrew G. Grubbs, et al.). The specimens are in the Florida State Collection of Arthropods, Gainesville.

Diagnosis.—At present, the only known troglotic member of the genus in California; distinctly larger and more attenuated than the common epigean forms, with palpal femur more than 0.7 mm long, about 5.5 times as long as broad; with only two eyes.

Description.—Male and female quite similar, but female larger. With the general features of the genus (see Muchmore and Benedict 1976). All sclerotized parts tan.



Figs. 1-3.—*Apochthonius grubbsi*, new species: 1, a coxal spine showing anterior projection of base; 2, dorsal view of right palp; 3, lateral view of left chela.

Carapace a little longer than broad, narrowed posteriorly; with small denticulate epistome; two corneate eyes; chaetotaxy 8-4-4-2-4=22. Abdomen typical; tergal chaetogenital opening in a single irregular row; anterior sternites of female 8:(3)8(3):(3)7(3):9:9:-. Coxal chaetotaxy 2-2-1:3-0-CS:2-2:2-3:2-3; each coxa I with three spinelike setae of the usual kind, all their bases having well developed anterior spurs (Fig. 1).

Chelicera about 0.85 as long as carapace; hand with seven setae; each finger with a few irregular teeth; spinneret a small elevation in both male and female; flagellum apparently of eight pinnate setae.

Palp slender (Fig. 2); femur 1.2 and chela 1.7 times as long as carapace; trochanter 1.95-2.1, femur 5.35-5.65; tibia 2.25, and chela 5.6-6.2 times as long as broad; hand 1.95-2.05 times as long as deep; movable finger 1.95-2.05 times as long as hand. Trichobothria in the usual positions (Fig. 3). Fixed chelal finger with 72-78 and movable finger with 62-63 contiguous marginal teeth; movable finger with a sensillum near the dental margin midway between *st* and *sb*.

Legs rather slender; leg IV with entire femur 2.8-3.0 and tibia 4.9-5.3 times as long as deep. Tactile setae of the usual kind on tibia and tarsi of leg IV.

Measurements (mm): Figures given first for male, followed in parentheses for those of female. Body length 1.73(2.03). Carapace length 0.58(0.64). Chelicera 0.47(0.58) by 0.245(0.30). Palpal trochanter 0.26(0.27) by 0.125(0.14); femur 0.71(0.75) by 0.125(0.14); tibia 0.34(0.385) by 0.15(0.17); chela 0.99(1.12) by 0.16(0.20); hand 0.33(0.385) by 0.16(0.20); movable finger 0.68(0.75) long. Leg IV; entire femur 0.60(0.695) by 0.215(0.23); tibia 0.45(0.51) by 0.095(0.095); metatarsus 0.215(0.245) by 0.07(0.075); telotarsus 0.40(0.43) by 0.045(0.05).

Etymology.—The new species is named for Andrew G. Grubbs who collected these and many other specimens in Californian caves.

Remarks.—This is the first cave-adapted *Apochthonius* to be found in California. Other troglobitic members of the genus are known from eastern and central United States (see Muchmore 1976) and two with troglobitic tendencies have been described from southeastern and central Oregon, *A. malheuri* Benedict and Malcolm (1973), and *A. forbesi* Benedict (1979). *A. grubbsi* is easily distinguished from the Oregon species by the possession of only 22 setae on the carapace. It seems most like the epigean form, *A. maximus* Schuster (1966), in that the setae on each side of the male genital opening are modest in number (8-10) and lie in a single, though irregular, row.

Music Hall Cave, the type locality of this species, is also the type locality for new species of *Larca* and *Pseudogarypus* (Muchmore, in preparation). Other cave adapted pseudoscorpions have been found in nearby caves in Calaveras and Tuolumne Counties, including *Neochthonius troglodytes* Muchmore (1969a), *Microcreagris grahami* Muchmore (1969b) and a new species of *Aphrastochthonius* (Muchmore, in preparation). These caves obviously have been a good place for isolation and speciation, at least for pseudoscorpions.

William B. Muchmore, Department of Biology, University of Rochester, Rochester, New York, 14627.

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BOOK REVIEW

The Crab Spiders of Canada and Alaska: Araneae: Philodromidae and Thomisidae, by Charles D. Dondale and James H. Redner, 1978. Part 5 of The Insects and Arachnida of Canada, Publication 1663, pp. 1-255, 725 figs., 66 maps. Available from Printing and Publishing Supply and Services Canada, Hull, Quebec, Canada K1A 0S9, Canada. Canada: \$7.50; other countries: \$9.00.

This handsome, soft-bound volume, dealing with the spider families Philodromidae and Thomisidae from north of the United States, is a striking contribution to Canadian arachnology. About half of the taxa of all temperate North America (110 of some 223 species) occur in Canada. The authors have drawn much of the data from their many papers on these spiders, but this has been materially supplemented by new appraisals, illustrations, and distribution information. The work is preceded by resumes of anatomical details and a key to the families known from north of the United States. This section, rather copiously illustrated, suggests that works on other families will follow the present volume to offer new insight into the wealthy but still only moderately exploited spider fauna of Canada. The work offers a Glossary of terms and an excellent Bibliography which will be found useful to all grades and kinds of spider students.

The philodromid crab spiders are swift runners that forage actively over ground and plant substrata. Their laterigrade aspect is less evident than that of the thomisids with which they were long placed as a subfamily. Much still remains to be learned about their natural history. The 47 species found in Canada include ten species well known in Europe and northern Palearctica and these are also long residents of North America. Two other species (*Philodromus dispar* and *Thanatus vulgaris*) are more recent immigrants brought in by trade but these are now established in North America.

The spiders of the family Thomisidae are more crablike and less active than the philodromids and excell as ambushers, easily overpowering large insects. The natural history of some of the ambushing flower spiders, notably *Misumena vatia*, which is as common in Europe as in North America, is rather well known but much still remains to

be learned about these friendly little spiders. The thomisids of Canada (about 63 species are so far known) have much in common with those of Europe but only four species seem to be the same. The ranges of all these suggest that they are long residents of both regions.

The present work is largely a systematic review of the Canadian crab spider fauna with good keys for the various genera, succinct descriptions of each sex, and a variety of informative comments. The distribution maps are especially instructive and in some of these we find index of rarity, or wide range and coverage of such vast areas. The genitalic illustrations are printed in good size and portray in excellent fashion the distinctions between species. I have found the information of this book easy to use and believe that biologists of many persuasions and beginners as well will find it useful. Precise identification is the first step toward deeper researches into the biology of the crab spiders and it is available in this work for all North Americans.

Willis J. Gertsch, Curator Emeritus, American Museum of Natural History, New York.

NOMENCLATURAL NOTE

Opinion 1119 of the International Commission on Zoological Nomenclature placed the names *Amaurobius* C. L. Koch, 1837 with the type species *Clubiona atrox* Latreille, and *Coelotes* Blackwall, 1841 with the type species *Clubiona saxatilis* Blackwall on the Official List of Generic Names in Zoology, and placed the names *Amaurobius* C. L. Koch, 1836, *Cavator* Blackwall, 1840, *Ciniflo* Blackwall, 1840, and *Caelotes* Blackwall, 1849, on the Official Index of Rejected and Invalid Generic Names in Zoology. The name *Amaurobiinae* is placed on the Official List of Family Group Names in Zoology, and the name *Ciniflonidae* on the Official Index of Rejected and Invalid Generic Names in Zoology. (Bull. Zool. Nomencl. 35: 216-220, 1979.)

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The Eastern and Western sections of the Society hold regional meetings annually, and every three years the sections meet jointly at an International meeting. Information about meetings is published in *American Arachnology*, and details on attending the meetings are mailed by the host(s) of each particular meeting upon request from interested persons. The next International meeting will be held during the summer of 1981, and is scheduled to take place at The University of Tennessee, Knoxville, Tennessee. The 1980 regional meetings are scheduled as follows:

Eastern Section

Dr. George Uetz
Department of Biology
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Dates: 19-22 June 1980

Western Section

undecided

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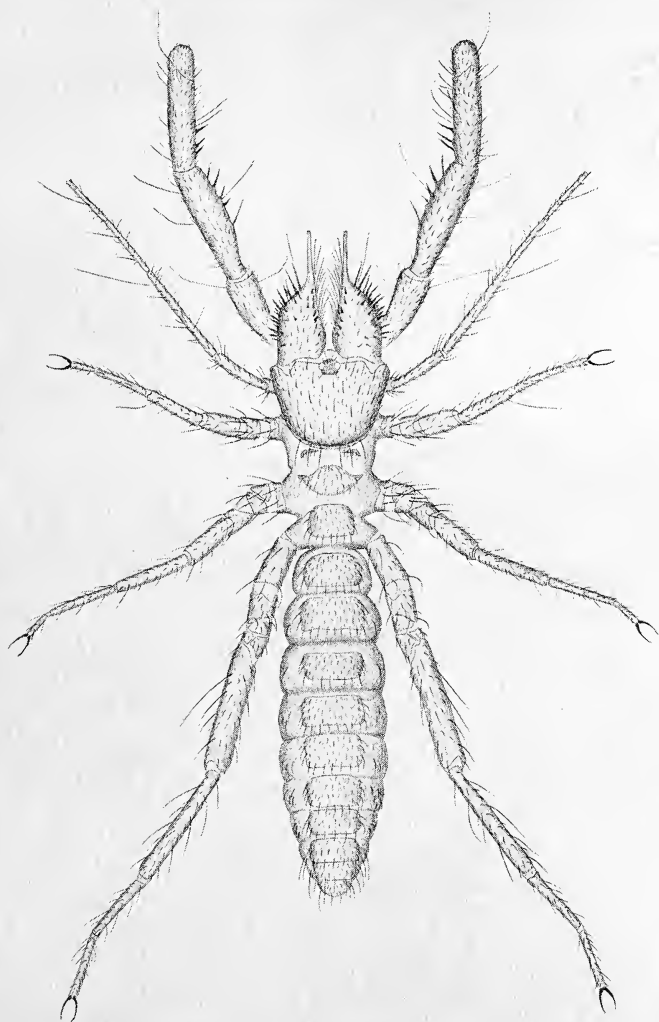
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**THE ERIGONINE SPIDERS OF NORTH AMERICA.
PART 1. INTRODUCTION AND TAXONOMIC BACKGROUND
(ARANEAE: LINYPHIIDAE)**

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ABSTRACT

This introductory paper on North American erigonine spiders reviews the evidence for the hypothesis that the erigonines form part of the family Linyphiidae, and maintains that a strict subdivision of the family into two phylogenetically pure branches is not feasible on current data. The structure of the male palpal organ is briefly described, and its importance in the taxonomy and phylogeny of the erigonines is stressed. Other characters used in erigonine taxonomy are briefly mentioned.

INTRODUCTION

The author is proposing to undertake the revision of a number of North American genera of erigonine spiders, based mainly on material from the American Museum of Natural History (New York), the Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts), and the Canadian National Collection (Ottawa). It is hoped that the publication of the results will encourage others to take up the collection and study of this somewhat neglected group of spiders.

In the literature, both American and European, the erigonine spiders have often been placed in a separate family, the Erigonidae or Micryphantidae; if a family name is required, Erigonidae now seems to be preferred (Platnick and Levi 1973). The erigonine spiders are, however, regarded by many arachnologists as forming part of the family Linyphiidae; this hypothesis is not universally accepted, but in my opinion there is substantial evidence to support it (see later).

The North American erigonines have been studied and described by a number of authors, particularly by Emerton, Banks, Crosby and Bishop. Chamberlin and Ivie, and more recently by Dondale, but the majority of the descriptions are now quite old and somewhat inadequate by modern standards. The number of erigonines so far described from this geographical area, from the arctic far north to the sub-tropical south, does not much exceed 500 species, quite a few of which are known from one sex only. This number is close to the number of species known from Europe, but the European erigonines have been more thoroughly collected and investigated, and there are very few species of which both sexes are not known. There can be no doubt whatever that many new species remain to be discovered in North America.

The erigonines are not a particularly easy group for the taxonomist, and this is one of their attractions. Their small size (1-3 mm in total length) and the large number of species (particularly in northern latitudes) increase the taxonomic problems, but the difficulties should not be over-stressed. There are now keys, admittedly not completely reliable, for diagnosing most of the genera of the European erigonines, and there is no reason why similar keys should not be constructed at a later date for the North American genera. It is to be noted that many European genera are not represented in North America (except possibly in Alaska and northern Canada) and that many North American genera are not present in Europe.

The spiders of the family Linyphiidae (s. lat.) have a very generalised morphology. There appears to be no somatic character of combination of somatic characters which can be used to formulate a rigid definition of this family, which is distinguished from other families mainly by the *absence* of the somatic characters which are used to define these families. The one character which can be seen to distinguish the Linyphiidae from all other families is the structure of the male palpal organ. As a consequence of the generalised morphology, the female erigonines offer in most cases greater taxonomic and diagnostic problems than the males, which often exhibit striking secondary sexual characters. Only in rare instances can sub-adult erigonines be identified to species or even generic levels.

STRUCTURE OF THE MALE PALP IN THE LINYPHIIDAE

The structure of the male palpal organ has been well described by previous authors (particularly by Merrett 1963; see also Saaristo 1971), but in view of its importance in linyphiid taxonomy and phylogeny a brief account of the structure, including some new data, is given here.

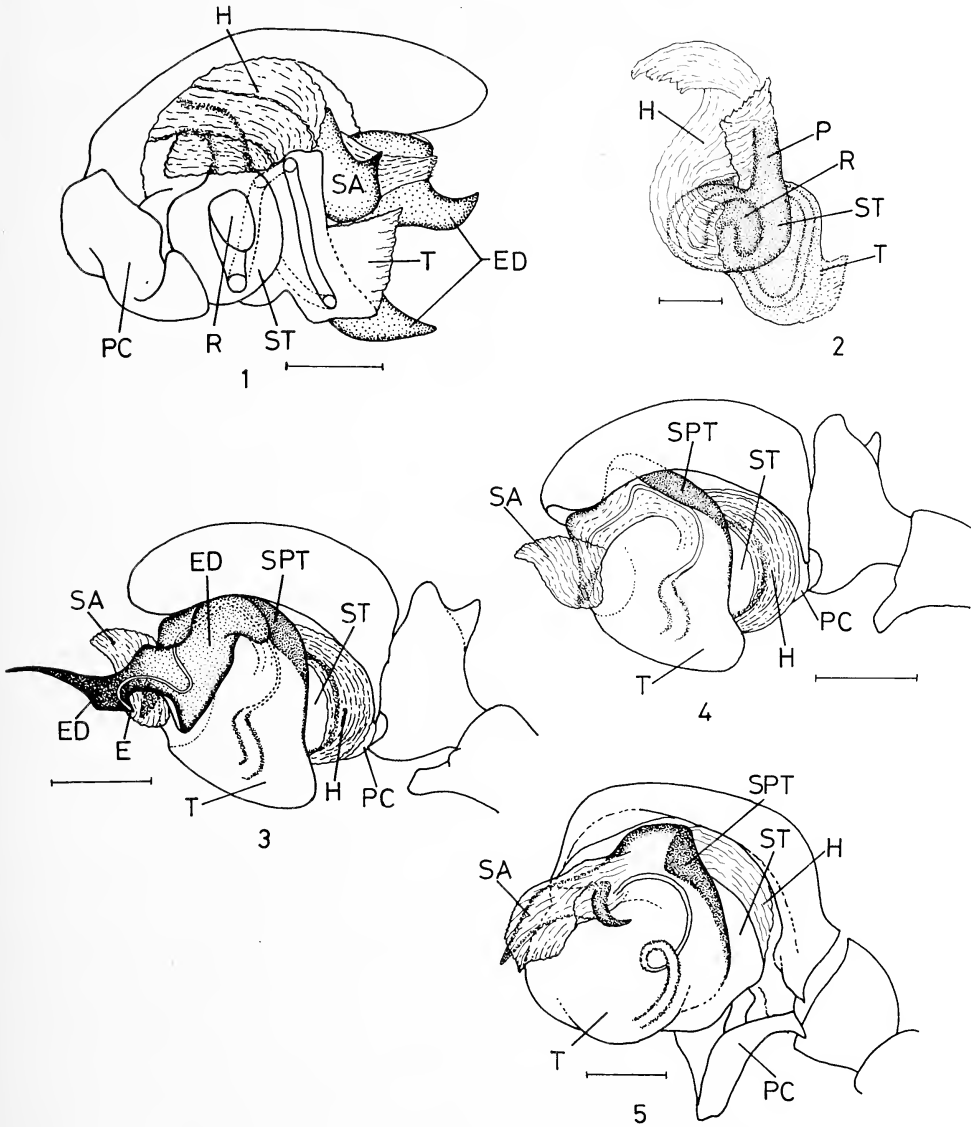
The palpal tarsus (cymbium) has a more or less flat paracymbium, which is articulated to the cymbium and lies adjacent to the ectal side of the palpal organ. This paracymbium is basically U-shaped (e.g. Fig. 9), but there is considerable variation in the detail; the paracymbium is usually, but not always, more complex in the linyphiines than in the erigonines.

The components of the palpal bulb are as follows:

(i) **The (basal) haematodocha.**—This is not a simple distensible sac as sometimes depicted, but an irregular thin-walled elastic tube coiled around the “subtegular petiole” [see (ii) and Figs. 1, 2]. This tube is attached at its basal end to the alveolus and at its distal end to the subtegulum. The haematodocha is collapsed and flattened in the unexpanded bulb, and is then practically invisible except in some cases for a small part of its distal end where it is attached to the subtegulum (Figs. 3, 4, 5). The spiral form of the haematodocha can readily be verified: after soaking the palp in 5% aqueous glycerol to soften it, the bulb can be pulled away from the cymbium with fine tweezers to reveal the coiled elastic haematodocha.

(ii) **The subtegulum.**—This sclerite is not a simple ring, but is shaped more like a shallow circular box with a short handle. The “handle”, which arises ecto-dorsally from the subtegulum (Figs. 1, 2), runs up into the alveolus and appears to be attached at its distal end to near the basal end of the haematodocha, the point of attachment being towards the ectal side of the cymbium. I propose the descriptive label “subtegular petiole” for this projection from the subtegulum. The haematodocha forms a short spiral round the petiole, and is fastened to the subtegulum on the posterior and mesal sides in the unexpanded palp (Figs. 2, 3).

(iii) **The tegulum.**—This is a sac of variable shape which is joined to the subtegulum over a relatively small area where the seminal duct passes from the subtegulum into the tegulum. There is a more or less sclerotized projection arising from the tegulum, the suprattegulum (Saaristo 1971; this is referred to by Merrett 1963, as the “median apophysis”). In the unexpanded palp, the suprattegulum is situated on the mesal side



Figs. 1-5.—Male palps: 1, *Eperigone tridentata* (Emerton), ectal, with part of cymbium cut away to show coiled haematodocha; 2, *Eperigone tridentata*, bulb detached from cymbium, viewed from behind: ED removed; 3, *Ceratinopsidis formosa* (Banks), mesal; 4, *Ceratinopsidis formosa*, mesal, ED removed; 5, *Leptyphantès zimmermanni* Bertkau, mesal, ED removed. Abbreviations: E, embolus; ED, embolic division; H, haematodocha; P, subtegular petiole; PC, paracymbium; R, reservoir; SA, suprattegular apophysis; SPT, suprattegulum; ST, subtegulum; T, tegulum (Scale lines 0.1 mm).

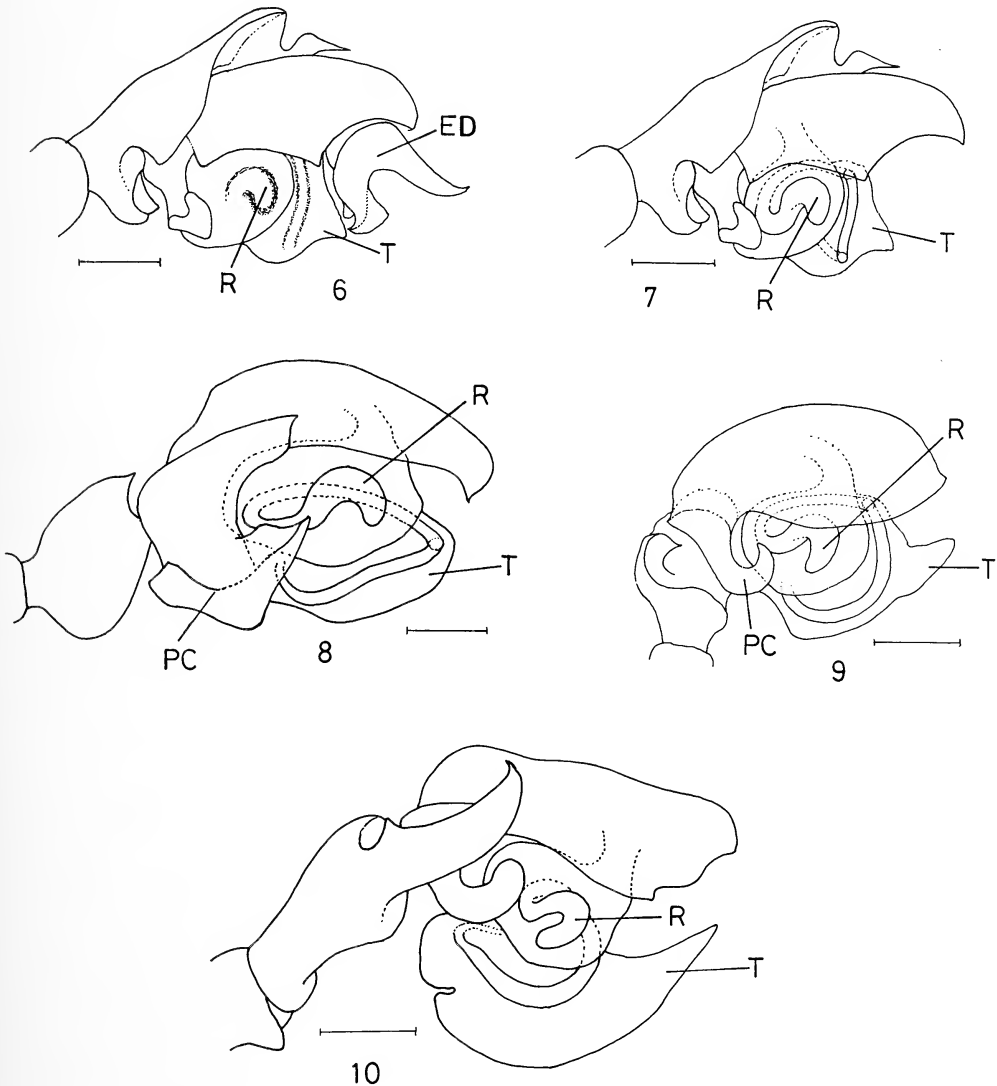
(Figs. 3, 4, 5), lying approximately along the junction between the subtegulum and the tegulum. In this position it does not have the appearance of a projection from the tegulum, but when the palp is expanded the construction becomes clearer. At its anterior (distal) end the suprattegulum carries an apophysis, the suprattegular apophysis (SA). This apophysis, which in the erigonines is often membranous, has a variety of forms ranging from the very simple to the relatively complex; in some species the apophysis may arise both from the end of the suprattegulum and from the stalk [see (iv)]. In some species there is a separate small membranous apophysis arising from the region of the stalk. The tegulum varies a good deal in shape, both in the linyphiines and in the erigonines, and may have membranous projections, particularly anteriorly.

(iv) **The embolic division (ED).**—This is a separate sclerite which carries the embolus, and is attached to the suprattegulum by a membranous stalk (Saaristo 1971, calls this the "column"). The ED is complex in form in typical linyphiine species, e.g. *Leptyphantès* Menge; it is simpler, though very variable in shape, in the typical erigonine species. The form of the ED is of prime importance for species determination, particularly in the linyphiines but often too in the erigonines; it is also valuable for the assessment of generic and suprageneric relationships. Some of the numerous forms of the ED in European species are figured by Merrett (1963).

The reservoir of the sperm duct lies in the subtegulum and is attached to its ectal wall: the marking usually visible on the subtegulum just in front of, or partially obscured by, the paracymbium (e.g. R, Fig. 6), is the area of attachment of the reservoir. This reservoir is shaped like an inverted U, with the closed end anterior (Fig. 7). From the reservoir, the duct (usually rather smaller in diameter than the reservoir) runs in an irregular spiral through the subtegulum and into the tegulum; it then runs down through the tegulum on the ectal side and finally up again on the mesal side, to enter the ED by way of the suprattegulum and the stalk (Figs. 3, 4). The reservoir seems always to be in the form of an inverted U, and the path followed by the duct is always essentially that described; this is true for all the numerous linyphiine and erigonine species I have examined, including species from Europe, North America, South America, Central Africa, Australia and New Zealand. While the form of the reservoir and the conformation of the duct appear to be essentially constant within the family, there are of course small differences in the detail. For example, in some genera, both linyphiine (e.g. *Centromerus* Dahl, Fig. 8) and erigonine (e.g. *Ceratinella* Emerton, Fig. 9), the subtegulum and tegulum are positioned more horizontally than in many erigonines, but the duct conformation is basically the same with the difference that the axis of the spiral is inclined more to the vertical than to the horizontal. Even in palpal organs which appear somewhat abnormal in construction (e.g. in *Gnathonarium* Karsch, Fig. 10) the basic duct conformation remains unchanged. In *Erigone* Audouin and some other genera the reservoir, instead of lying in the "normal" position, has been rotated through up to 90°, so that only one arm (the closed end) of the reservoir is adjacent to the ectal wall of the subtegulum (e.g. *Eperigone* Crosby and Bishop, Fig. 1); apart from this small change, the duct conformation is normal. In addition to these minor variations, the duct itself may have small twists or convolutions within the tegulum (e.g. Fig. 5).

A brief mention must be made of the expansion of the palpal organ. The supply of blood to the subtegulum, required to raise the pressure and bring about ejection of sperm from the reservoir, is probably by way of the subtegular petiole, which seems to be the only part of the subtegulum which is open (via the basal end of the haematodocha) to the blood supply in the cymbium. When the coiled haematodocha is expanded, by an increase

in the internal pressure, it tends to uncoil. The attachment of the subtegular petiole to the base of the haematodocha on the ectal side restricts the movement of the subtegulum, so that the expanding haematodocha repels the bulb from the cymbium mainly on the mesal side, and at the same time imparts some rotation to the bulb. As a result, the ED moves from the mesal side to the front of the palp or even towards the ectal side. When the embolus is fixed in the epigyne prior to expansion, a degree of rotatory movement may be imparted to the ED, possibly facilitating insertion.



Figs. 6-10.—Male palps: 6, *Diplocephalus cristatus* (Blackwall), ectal; 7, *Diplocephalus cristatus*, ectal, ED removed, cleared; 8, *Centromerus arcanus* (O.P.-Cambridge), ectal, ED removed, cleared; 9, *Ceratinella brevis* (Wider), ectal, ED removed, cleared; 10, *Gnathonarium dentatum* (Wider), ectal, ED removed, cleared. Abbreviations: ED, embolic division; PC, paracymbium; R, reservoir, T, tegulum (Scale lines 0.1 mm).

THE LINYPHIIDAE AS A MONOPHYLETIC GROUP

The palps of typically linyphiine and typically erigonine spiders appear at first glance to be very different. Closer examination, however, shows that the differences are not in the basic construction of the palpal bulb, but only in the detail. The chief distinctions between the two forms are: (i) the embolic division is notably more complex in form in the linyphiines than in the erigonines; (ii) the supratégular apophysis is frequently more complex in the erigonines than in the linyphiines. When the embolic division is removed from the palpal organ, by breaking off at the stalk, the agreement in basic construction between linyphiine and erigonine palps becomes clear, the same structural components being present in each case (Figs. 4, 5; 8, 9).

The presence of the paracymbium as a separate articulated sclerite, the basic structure of the palpal bulb (i.e. haematodocha, subtegulum, tegulum, supratégulum with supratégular apophysis, embolic division as a separate sclerite), the form of the seminal reservoir and the route of the duct to the embolus via the supratégulum, represent a conglomerate character which is almost certainly apomorphic, having been derived either by elaboration of a more simple palpal structure (most likely) or by reduction of a more complex structure (less likely). So far as I know, this combination of characters is not present in any other branch of Araneoidea. On the basis of Hennig's reasoning (Hennig 1966), the presence of this synapomorphic character, or conglomerate of synapomorphic characters, carried by all species without any currently known exceptions, offers substantial support to the hypothesis that the family Linyphiidae (s. lat.) is a monophyletic group.

SUBDIVISIONS OF THE FAMILY

It was pointed out above that there are no somatic characters which suffice to define the family Linyphiidae. It is also true that the two groupings into which the family has usually been split, namely the subfamilies Linyphiinae and Erigoninae, cannot be defined in a scientifically acceptable manner by any combination of somatic characters. The separation of the linyphiines and erigonines (whether as separate families or as subfamilies) has in the past been carried out almost entirely on the basis of the dorsal tibial spines (of the female), the linyphiines having two spines on tibia IV while the erigonines have one (or occasionally zero). For the European fauna a more recent formula has been that those species which have *either* two dorsal spines on tibia IV *or* one dorsal spine on tibia IV plus one dorsal spine on metatarsi I and II, are linyphiine, the remainder being erigonine. This device does on the whole separate the linyphiines (with more complex palpal organs) from the erigonines (with less complex palpal organs), but it also throws up a number of anomalies: in particular, some species with the rather simple palpal organs characteristic of the erigonines are by this formula placed with the linyphiines.

It has been suggested (Blest 1976) that it may be possible to split the Linyphiidae into two groups or subfamilies on the basis of the tracheal arrangements; typical linyphiines have four simple tracheae which are confined to the abdomen, while typical erigonines have two short simple lateral tracheae and two large medial trunks which divide into numerous small branches before passing as two bundles into the cephalothorax. Division of the family on this basis does not however appear to be clear cut, and leaves a number of questions unresolved: this was emphasized by Blest and Pomeroy (1978) after their study of some aspects of the primitive genus *Mynoglenes* Simon, which possesses a mixture of linyphiine and erigonine characters, including the linyphiine type of tracheal system.

One problem which complicates the division of the Linyphiidae into two subfamilies is that although the majority of species have palpal organs which are clearly either linyphiine or erigonine in complexity, there is a sizable minority of species where the palpal organs are intermediate and do not clearly fall into either category. No taxonomist has so far been able to define the features of linyphiine and erigonine palps in such a way that all species can be placed unequivocally into one group or the other. Blest (1976) has argued that some of the intermediate palpal forms, and indeed some of the forms normally regarded as erigonine, may have been produced by reduction of the more complex (linyphiine) forms. I have suggested (Millidge 1977) that the contrary development may have taken place, and that some of the intermediate and the more complex palpal forms may have been derived by elaboration of the more simple forms. In the present state of our knowledge of the evolution of the family, it is probably sensible to accept that both processes may have taken place at different times.

Lehtinen and Saaristo (1970) and Lehtinen (1975) have also put forward the view (without however detailing the evidence on which the view was based) that the simple bifurcate splitting of the Linyphiidae is not a tenable hypothesis.

On the data available at the present time it seems clear that there is no good scientific basis (synapomorphy) for dividing the family into the two traditional groupings, the Linyphiinae and the Erigoninae. Nevertheless the terms "linyphiine" and "erigonine" are still useful descriptive labels and can continue to be used, provided that it is understood that they refer, somewhat loosely, to structural characteristics rather than to phylogenetic relationships (Millidge 1977).

The history of the many attempts to split the erigonines into suprageneric groups (often in the past designated as subfamilies of the Erigonidae) has been summarised by Merrett (1963) and will not be repeated here. It is sufficient in this paper to indicate that there is no scientific justification for splitting the erigonines into the historical suprageneric groups such as Masonini, Pelecopsini (Lophocarenini), Gonatiini, etc. The characters on which these groups were based [e.g. stout ventral spines on the anterior legs (Masonini), presence of trichobothria on metatarsus IV (Gonatiini)], are very probably not apomorphous and thus not valid for establishing phylogenetic relationships in the groups concerned. Few if any of the suprageneric categories so far proposed by various authors for the erigonines or linyphiines have been scientifically based on the presence of identified synapomorphic characters.

To sum up, there appears to be no alternative for the present but to leave unresolved the important problem of how to subdivide the Linyphiidae into phylogenetically valid subfamilies or other suprageneric groups. The wide differences which exist in the detail of the male palpal organ (particularly of the embolic division), coupled with the differences in the tracheal structures, indicate that most probably the family has evolved along several distinct lines, but there are insufficient data as yet to allow these branches of the family to be recognized and defined with any certainty. If taxonomy is to be regarded as science rather than art, then taxonomists must adhere to scientific disciplines: proposals for suprageneric categories (and indeed for new genera) should be treated as scientific hypotheses, which must be supported by fully disclosed data and reasoning. The erection of properly defined suprageneric groups in the Linyphiidae will perhaps only be possible when our knowledge of the global linyphiid fauna has been further extended, and the data have been subjected to a fresh analysis and interpretation.

CHARACTERS USED IN THE DEFINITION AND DIAGNOSIS OF GENERA IN THE ERIGONINES

(i) **Genitalia.**—At the present time, the most reliable character for defining the erigonine genera is almost certainly the structure of the male palpal organ. In an earlier paper I discussed the possible value of this character for establishing phylogenetic relationships (Millidge 1977). The palpal organ in the Linyphiidae is geometrically fairly complex, and it is considered improbable that the structure ("conformation") present in a given species or group of species will have been evolved on more than one occasion. In addition, the palpal organ is present in the male sex only for a limited period of the life span of the spider, and it is unlikely therefore that this organ will have been much influenced by purely environmental factors. On the basis of these premises it was put forward as a hypothesis (Millidge 1977) that the palpal conformation of erigonine spiders is an apomorphic character in the Hennig sense. Thus it should be possible, in the Linyphiidae in general, and in the erigonines in particular, to define genera as phylogenetic entities on the basis of some feature or features in the structure of the palpal organs. In this series of papers on the North American erigonines, attempts will be made to define the genera on the basis of the palpal structure together with any other character which may appear to be appropriate.

The spiders of some genera (e.g. *Erigone*) have epigyna which are fairly characteristic in appearance and which can be useful for diagnosing the genus of female specimens. The internal genitalia associated with the epigynal plate, i.e. the spermathecae and associated ducts and structures, as seen by clearing in clove oil or other suitable liquid, do not appear to be particularly complex in structure in the erigonines, and hence offer fewer characters of potential value for taxonomy than do the palpal organs. Examination by clearing in this simple way, however, cannot show up all the detail of the internal structure, and the development of more sophisticated techniques may reveal additional details and complexities. Although recognition of the genus is sometimes possible by the form of the epigynum, it is probably true that at the present time there is no instance where an erigonine genus can be satisfactorily defined on the structure of the epigynum or of the internal genitalia. It seems probable that the determination of phylogenetic relationships by means of the female genitalia, when and if this becomes possible, will be based on a combination of the form of the genital plate coupled with the structure of the internal parts, i.e. will be based on the structure of the whole genitalia.

(ii) **Chaetotaxy and other numerical characters.**—As an aid to identification, the chaetotaxy of the erigonines has proved a very useful character for the European species. There is currently insufficient information to judge whether this character will be equally useful for the North American fauna. The chaetotaxic characters most frequently used are the dorsal tibial spines and the metatarsal trichobothria.

The tibial spines (macrosetae) are usually quite distinct from the hairs (setae), being both longer and thicker; occasionally, when the spines are rather thin and short, differentiation can be more difficult. The tibiae in female erigonines normally have one or two dorsal spines, but in a few species spines may be completely absent (or indistinguishable from hairs). The number of dorsal tibial spines present is expressed by the formula $abcd$, where a is the number on tibia I, b the number on tibia II, etc. For the females, the formula is most frequently 1111, 2211 or 2221, but occasionally it is 0000 or 2222. The male sometimes has the same spinal formula as the female, but often the spines may be shorter and weaker or entirely absent, particularly on legs I and II.

The trichobothria are long fine hairs arising from the center of a circular pit which, under the magnifications commonly used with the light microscope, appears as a small circle. In the Linyphiidae, the metatarsi of legs I-III have one trichobothrium each, on the dorsal side, while that of leg IV has one or none; there are a few instances among the linyphiines where the metatarsi have more than one trichobothrium, particularly on leg I, but no such case among the erigonines, so far as I know. The presence or absence of the trichobothrium on metatarsus IV is sometimes of taxonomic value. The position of insertion of the trichobothrium on the metatarsus shows only small variation within a species, and often also within a genus, at least in the European genera. The method of expressing the location of the trichobothrium is shown in Fig. 11, where the position is given by the expression: TmI (i.e. position on metatarsus of leg I) = a/b , expressed as a decimal fraction. The variation in the value of TmI within a species is probably up to $\pm 10\%$, but even so this function can often be useful in diagnosis. The position of a leg spine can be expressed in a similar way if desired.

The leg spines are fairly readily lost if the specimens are shaken around in large vials, and unfortunately this has sometimes been the case with museum specimens. The trichobothria are lost less readily, and even when they have broken off the small pit at their base is almost always visible, even in old and faded specimens.

The chaetotaxy (tibial spines and metatarsal trichobothria) is often fairly constant within probably good genera, but by no means invariably so. Thus although useful for diagnostic purposes, this character cannot be regarded as a reliable one for deciding phylogenetic relationships.

The number of trichobothria present dorsally on the palpal tibia, of either sex, can in some instances be of diagnostic value.

It may on occasions be found useful for diagnosis to record a few other characters expressed numerically, e.g. the stoutness of the legs as given by the ratio: length/diameter (l/d) of a leg segment (Fig. 11), the ratio of length of one leg segment to another, etc.

(iii) **Male palpal tibia and male carapace.**—In some genera the male palpal tibia has a fairly constant basic form, which differs only in detail from species to species. In other genera (which may or may not be monophyletic) the tibia shows a wider degree of variation. The form of the tibia should therefore be used with caution as a indicator of relationship.

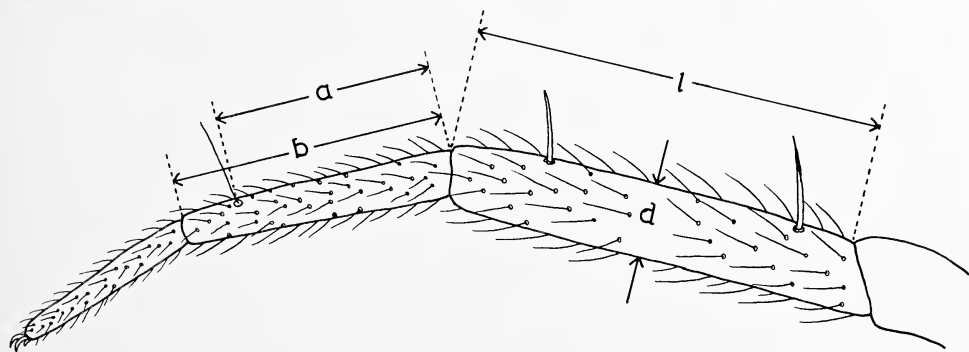


Fig. 11.—Part of leg I of erigonine spider, to illustrate the methods used for expressing (i) the position of the metatarsal trichobothrium, and (ii) the length/diameter (at mid-point) of tibia - see text. (i) $TmI = a/b = 0.80$; (ii) $Tibia\ I\ l/d = ca. 5.5$

In the past, the form of the male carapace (the type and shape of protuberances, etc.) has often been used by arachnologists to define genera. Within what now appear to be properly defined genera, however, more than one type of protuberance may frequently be encountered. As with the male palpal tibia, therefore, this secondary sexual character should likewise be regarded as of questionable value for genus definition.

(iv) **Tarsal claws.**—The form of the tarsal claws is occasionally useful in diagnosis. There are a few genera in which these claws are distinctly pectinate, that is they are furnished with a comb of long teeth: this is the case for example in the genera *Walckenaeria* Blackwall, *Gonatium* Menge and *Tapinocyba* Simon. Although sometimes a useful taxonomic character, which can be used to confirm the generic position of a species, the pectinate claws are probably of little phylogenetic value, since the pectination is probably a primitive character which has occasionally been retained.

(v) **Eyes and cheliceral teeth.**—Because of the paucity of distinguishing characters visible in the erigonines, the earlier arachnologists made frequent use of the cheliceral teeth (number and size) and of the eyes (size, spacing and curvature of the rows) for genus definition. These characters are not only difficult to measure accurately, but seem to show too much individual variation to be of any real value, at least above the species level.

DESCRIPTIONS OF ERIGONINE SPECIES

As stated earlier, the erigonine spiders are very generalised in form, apart from some sexual characters. Long descriptions (e.g. of color, leg lengths, cheliceral teeth, eye size and spacing, etc.) are usually of little or no diagnostic value and are unnecessary for most purposes. In this series of papers I propose therefore to keep the descriptions of the species as brief and economical as possible, concentrating on the characters useful for diagnosis. The work to be reported will be based almost entirely on museum specimens, in some of which the colors have faded, and in which increasing transparency has sometimes changed the appearance of the epigyna from those of fresh specimens: these points should be borne in mind when use is made of the descriptions.

GENERAL

In order to prevent the loss of limbs, spines and trichobothria, which are diagnostically useful, erigonine spiders should not be stored loose in large vials. They should be kept in alcohol, out of bright light (which catalyses oxidation and bleaching), in small vials, e.g. 25-40 mm long by 5-8 mm diameter, which are placed in alcohol in larger vials or bottles. In small vials the spiders suffer less damage when the storage bottles are moved or shaken, e.g. when sent through the mail. If a palp or epigynum is detached (sometimes necessary for identification), it should be stored in a separate small vial and labelled. The small vials employed for storage may be plugged with cotton wool or preferably with a polyethylene closure; the larger vials or bottles should be sealed against evaporation, and a polyethylene closure is also preferred here. The use of stoppers made of rubber (natural or synthetic) is to be discouraged, since the alcohol extracts from these rubbers some oily sulfurous material, which can produce cloudiness and an unpleasant smell in the alcohol in which the specimens are examined, and may also cause precipitation of troublesome dirt and sticky oil on to the specimens.

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THE ERIGONINE SPIDERS OF NORTH AMERICA. PART 2. THE GENUS *SPIREMBOLUS* CHAMBERLIN (ARANEAE: LINYPHIIDAE)

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ABSTRACT

A revision of the North American erigonine genus *Spirembolus* Chamberlin is reported. *Tortembolus* Crosby and *Bactroceps* Chamberlin and Ivie are synonymized with *Spirembolus*. "*Erigone*" *chilkatensis* Chamberlin and Ivie has been transferred to *Spirembolus*, while *Spirembolus chera* Chamberlin and Ivie, *S. cheronis* Chamberlin, *S. oreinoides* Chamberlin, *S. vasingtonus* Chamberlin (*nomen nudum*) and *Tortembolus approximatus* Chamberlin have been excluded from the genus. *Spirembolus orthus* Chamberlin is a synonym of *S. whitneyanus*. The genus *Spirembolus* is defined in this paper mainly on the basis of certain features in the structure of the male palpal organs; these palpal characters indicate that the genus is probably monophyletic. The female genitalia also show common characters. The revised genus contains 38 species, including the following 20 new taxa: *Spirembolus abnormis*, *S. dispar*, *S. elevatus*, *S. erratus*, *S. falcatus*, *S. fuscus*, *S. hibernus*, *S. humilis*, *S. latebricola*, *S. levis*, *S. mendax*, *S. mirus*, *S. montivagus*, *S. novellus*, *S. praelongus*, *S. prominens*, *S. proximus*, *S. pusillus*, *S. tiogensis* and *S. venustus*. The genus is sub-divided provisionally into three species groups, the *monticolens*, *spirotubus* and *tortuosus* groups. The genus appears to be limited to the western half of North America, but biological data are scarce. Descriptions, diagnoses and distribution maps are given for each species.

INTRODUCTION

As part of a programme of study of the North American erigonine fauna, the genus *Spirembolus* Chamberlin 1920 has been revised. The American Museum of Natural History, New York (AMNH) was the most important source of material for this study; much of this material had been provisionally sorted into genera, and sometimes species, by the late W. Ivie. Smaller amounts of material from the Museum of Comparative Zoology, Harvard University (MCZ) and from the Canadian National Collection, Ottawa, were also examined.

In the present revision the genera *Tortembolus* Crosby 1925 and *Bactroceps* Chamberlin and Ivie 1945 have been synonymized with *Spirembolus*, for reasons given later in this paper. The genus *Spirembolus* (in its original scope) has not been revised since 1945 (Chamberlin and Ivie 1945), while the genera *Tortembolus* and *Bactroceps* have not been revised since their original descriptions.

The genus *Disembolus* Chamberlin and Ivie 1933, said (Chamberlin and Ivie 1945) to be close to *Spirembolus*, is quite distinct and will be dealt with in a later paper.

GENUS *SPIREMBOLUS* CHAMBERLIN*Spirembolus* Chamberlin 1920:197*Tortembolus* Crosby 1925:115. NEW SYNONYMY*Bactroceps* Chamberlin and Ivie 1945:223. NEW SYNONYMY**Type species.**—*Cornicularia monticolens* Chamberlin 1919

Definition.—The members of this genus are small spiders with a total length of about 1-3 mm. The female carapace is unmodified, but in the male there are several different forms (e.g. Figs. 35, 137, 178). Where there is a distinct lobe present there are also holes behind the lateral eyes; the lobe does not carry the posterior median eyes. The eyes show no peculiarities except that in some males which have a lobe on the carapace they take up a *Pholcomma*-like configuration (Fig. 193). All the species have a file on the lateral margins of the chelicerae in both sexes. The abdomen is clothed with short hairs and is without scuta; in most cases it is more or less unicolorous, usually grey to black, but in a few species it has a clear dorsal pattern of white or pale colored bars or chevrons (Fig. 141). In some species there are clear striations on the epigastric plates (lung covers), usually more developed in the male than in the female; the coxae IV are equipped with tiny spurs, presumably for engaging these stridulatory files. The spur is often present, however, even in those species lacking the file. The legs are relatively short and stout, with a value for tibia I 1/d (females) of ca. 5 (range 4-7); the larger species tend to have the thinner legs. The legs have tibial spines (macrosetae) 2221 in the female (for definitions of formulae used, see Part 1: Millidge, 1980), most frequently reduced to 0021 or 0011 in the male; there are a few exceptions, e.g. *S. bilobatus* (Chamberlin and Ivie), which in most respects is close to other members of the genus, has tibial spines 1111 in the female. Metatarsi I-III have a trichobothrium, which is absent on metatarsus IV; the value of TmI is unusually variable from species to species within the genus, having a range of 0.35-0.80. In many of the species the first and second pairs of legs of the male have short curved hairs on the tibia and metatarsus (particularly on the dorsal side): these hairs are less developed or absent in some of the smaller species. The femur of the male palp is long, and the patella is often long also (e.g. Figs. 48, 65); but in some of the smaller species the patella is much shorter (Fig. 176). The males of a few species have a white bubble-like excrescence arising from the joint between the palpal femur and patella (Fig. 40). The palpal tibia of the male usually has a long apophysis, straight or curved, narrowed distally and with a small hook at the distal end (e.g. Figs. 1, 126); in addition, there is in many species a lower (inferior) apophysis (I, Fig. 30). The palpal tibia has 1, 2 or 3 trichobothria dorsally in the male, and 2 or 3 in the female (Figs. 132, 7, 30; 15, 38); when the female tibia has 3, the male tibia normally has 3 also, and when the female has 2 the male has 2 or 1. It is notable that in one species (*S. pachygnathus* Chamberlin and Ivie) the right tibia of the female has 3 trichobothria while the left has 2. The cymbium of the male palp is conical to a greater (Fig. 103) or lesser (Fig. 133) degree.

In common with most erigonines, the structure of the *Spirembolus* species is so generalised that it is impossible on the basis of known somatic characters either to define the genus or to differentiate it satisfactorily from related genera. The genus must therefore be characterised chiefly on the structure of the male palpal organ, which will now be described.

The paracymbium is elongate (Figs. 29, 48), somewhat as in the genus *Ceraticelus* Simon, but is less so in some of the smaller species (e.g. Fig. 189). The embolic division

(ED) consists of a spiral embolus of several turns (E, Fig. 32) with a short coiled tailpiece (T, Fig. 32); the coils of the tailpiece are less developed in some of the smaller species (e.g. Fig. 129). The sperm duct (made visible by clearing the palp in clove oil) runs down from near the anterior end of the suprategulum via the membraneous stalk to enter the ED from the mesal side, anterior to the tailpiece. The ED is of the same form in all species of the genus, but the embolus ranges from very long, with the terminal part thin and hairlike and forming a wide coil (e.g. Fig. 115), to short, with the distal part stouter and in a small coil (e.g. Fig. 95). In a few species the duct in the stalk runs posteriorly through one turn of the embolic coil before entering the embolus (Fig. 32). The suprategular apophysis (SA) is a membraneous ribbon which arises from the anterior (distal) end of the suprategulum but also has a membraneous connection with the stalk; there is a sclerotized strengthening section at its basal end where the SA arises from the suprategulum. The general form of the SA is shown in Figs. 29, 46; it runs in a curve along the anterior margin of the cymbium and then down the anterior edge of the tegulum on the ectal side. In living males the terminal part of the embolus probably rests on the SA, but is often detached from it in preserved specimens. The SA is of the same general form in all the species (Figs. 2, 46, 167, 180), but in those species with a short embolus it is shorter (Fig. 95). A small tongue-like membraneous apophysis arises from the surface of the tegulum near the base of the suprategulum (M, Fig. 46); this is present in all the species, but in many it is small and more or less hidden behind the ED. From other genera which have a coiled embolus and a coiled screw-like tailpiece (e.g. *Cochlembolus* Crosby, *Coreorgonal* Bishop and Crosby, etc. which will be dealt with in a following paper), *Spirembolus* is distinguished by the following characters: (i) the shape of the tailpiece: in some of the smaller *Spirembolus* species this is rather close to that in other genera; (ii) the form of the SA; (iii) the presence of the small tegular apophysis; (iv) the shape of the paracymbium. The characters (i) - (iii) are probably unique to the genus and are almost certainly apomorphic (derived); their presence in all the species supports the hypothesis that the genus as here constituted is monophyletic (Hennig 1966).

The female epigyna are all similar in form. Posteriorly there is a transverse chitinous plate, anterior to which the outlines of the spermathecae and internal ducts can be seen with a variable degree of clarity (e.g. Figs. 11, 56). Although the genus cannot be satisfactorily defined on the form of the epigynum, it is nevertheless possible with experience to recognize a *Spirembolus* female in most instances. The internal genitalia of the female (examined by clearing the excised epigynum, or occasionally the whole spider, in clove oil) appear to be similar in basic pattern in all the species. The sperm duct arises from an opening with thickened walls more or less on the mesal side of the spermatheca, and then follows a helical path around the dorsal to the ventral side of the spermatheca. Usually the helix is of one turn only (e.g. Fig. 58), but in some species having a long embolus there are several turns and/or additional convolutions (e.g. Fig. 22). In the case of some closely related species which form a series with decreasing lengths of emboli (e.g. *S. prominens*, new species, *S. monticolens* (Chamberlin) and *S. pachygnathus*: Figs. 6, 1, 4) the female genitalia show a corresponding reduction in the length and arrangement of the sperm duct (Figs. 22, 17, 20). In *S. erratus*, new species, and two related species, where the embolus is long to very long, the greatly lengthened sperm duct forms a helix of several turns (Fig. 165). These findings confirm that not only can the length of the male embolus increase or decrease substantially within a single genus but that the length of the sperm duct in the female can vary in a similar fashion.

The entrances to the sperm ducts leading to the spermathecae seem to be situated within the shallow depressions which are faintly visible (though often difficult to see) on

the epigynal plate (O, Figs. 104, 110). As is probably normal in the erigonines, the plate is folded under from the ventral to the dorsal side, forming a semi-transparent sclerotized envelope sealed at the sides but open anteriorly (on the inside) to the atrium. One female (probably of *S. spirotubus* (Banks)) had a broken-off embolus in the atrium, but this had been inserted under the side of the plate and was twisted erratically within the atrium. So far as could be ascertained, there are no entrances to the spermathecal ducts except from the ventral side of the plate. A broken-off embolus inside a female may thus not always be a reliable guide to the route of the spermathecal duct; it seems likely in the present case that the embolus had broken off because it had been inserted in the wrong position and become jammed behind the plate. Because of the transparency of the ducts, due to lack of pigmentation in some parts, it has not been possible in any species to trace with certainty the total pathway by which the embolus reaches (or approaches) the spermatheca from the external opening.

The generic names *Tortembolus* and *Bactroceps* are considered to be junior synonyms of *Spirembolus*. Only the form of the male carapace (a character which tends to be variable in other erigonine genera) would distinguish these genera from *Spirembolus*. The chaetotaxy (tibial spines and metatarsal trichobothria) of the *Tortembolus* and *Bactroceps* species is, with few exceptions, the same as in *Spirembolus*. In all three genera the male palpal organs are of closely similar pattern, with the same form of SA (Figs. 2, 46, 167, 180), and with similar ED's; the tailpiece in these smaller species tends to be more compressed than in the larger *Spirembolus* species, but in *T. fasciatus* (Banks) it is of the normal form (Fig. 150). The small tegular apophysis present in the *Spirembolus* males is also present in *Tortembolus* and *Bactroceps* (Figs. 167, 180). The female genitalia of *Tortembolus* and *Bactroceps* species also have the same general form as those of *Spirembolus*; this is illustrated by comparisons of *B. redondo* Chamberlin and Ivie (Fig. 188) with *S. perjucundus* (Fig. 73), of *B. bilobatus* Chamberlin and Ivie (Fig. 187) with *S. hibernus*, new species (Fig. 83) and of *T. fasciatus* (Fig. 159) with *S. humilis*, new species (Fig. 74). The stridulatory files on the epigastric plates, which are well developed in some *Tortembolus* species, are also present, albeit in weaker form, in a few of the *Spirembolus* species (e.g. *S. phylax* Chamberlin and Ivie, male).

The species "*Erigone*" *chilkatensis* Chamberlin and Ivie has also been moved into *Spirembolus*, on the evidence of the genitalia.

It is of interest to note that the species with the patterned abdomens (previously in *Tortembolus*) have in several instances a sibling form which has a unicolorous abdomen, but is otherwise closely similar. These distinct color forms, which have sometimes been found in the same localities as the unicolorous forms, are here regarded as separate species; biological data are needed to test this view. In the populations of *S. demonologicus* (Crosby) (unicolorous abdomen) and *S. pusillus*, new species (the sibling species with patterned abdomen) there are present in each case three distinct forms of the male carapace. In this paper it is assumed that the males of these two species are polymorphic, but it is perhaps not impossible that there are three species present in each of these populations; only one structurally recognizable female is present in each case.

The genus *Spirembolus* seems to have undergone rather vigorous speciation, in many instances accompanied by only minor structural change. Distinctions between species may rest, for example, on the diameter of the embolic coil, on the form of the male carapace, on the presence or absence of epigastric files, and on the presence or absence of an abdominal pattern. The structural differences, though often small, appear to be discrete: there seem to be no intermediates between the populations bearing these

characters. The existence of only small differences between some species results in a somewhat troublesome taxonomy. The females of a few species cannot be identified with certainty if captured without the corresponding male.

Examination of the types of all the previously described species shows that there has been confusion in the past over the identity of a few of the species. *S. spirotubus* (Banks) and *S. vallicolens* Chamberlin were completely confused by Chamberlin and Ivie (1945), while the *S. perjucundus* figured in the same paper is not *S. perjucundus* Crosby. In the key given by Crosby (1925) to the *Tortembolus* species only one species with a patterned abdomen was recognized (*T. fasciatus*), and probably in consequence all the patterned specimens in the AMNH Collection were labelled "*T. fasciatus*". In fact there are at least seven species which have the abdominal pattern, and most of the labelled specimens were wrongly identified.

Species.—The genus as defined in this paper contains 38 species, which are listed in Table 1. The holotype of *S. montivagus*, new species is deposited in MCZ; the holotypes of all the remaining new species are deposited in AMNH. All other specimens of the new species examined during this study rank as paratypes and are labelled as such; with few exceptions, these also are deposited in AMNH.

Species Groups—The species can be placed provisionally in three species groups, as shown in Table 1. These groups are as follows:

1. The *monticolens* group contains species with the following characters: two trichobothria are present on the palpal tibia (both sexes); the male palpal tibia lacks the inferior apophysis (e.g. Fig. 7); the curved hairs on the anterior legs of the male are only weakly developed.

2. The *spirotubus* group contains species with the following characters: three trichobothria are present on the palpal tibia (in both sexes); the male palpal tibia has an inferior apophysis in most cases (e.g. Fig. 30); the males have well developed curved hairs on the anterior legs.

3. The *tortuosus* group contains those species previously placed in *Tortembolus* and *Bactroceps* and related new species. They have the following characters: two trichobothria are present on the palpal tibia of the female, and one or two in the male (but *S. bilobatus* and *S. redondo* females sometimes have three); the males have a well developed lobe (or lobes) on the carapace with a hole behind the lateral eyes (e.g. Fig. 130); the male palpal tibia lacks the inferior apophysis (e.g. Fig. 157); the curved hairs on the anterior legs of the male are absent or very weakly developed; some species have a patterned abdomen; some species have strongly developed files on the epigastric plates.

These species groups may not be phylogenetically pure.

Misplaced Species—The following species do not belong in *Spirembolus*:

Spirembolus chera Chamberlin and Ivie 1933:20

This was synonymized, erroneously, with *Disembolus stridulans* Chamberlin and Ivie (Chamberlin and Ivie 1945); it will be dealt with in a later paper.

Spirembolus cheronus Chamberlin 1948:546

The type of this species has not been found, but from the figures given of the epigynum it cannot be a *Spirembolus*.

Spirembolus oreinoides Chamberlin 1948:546

The female holotype of this species has been examined; it is not a *Spirembolus*.

Spirembolus vasingtonus Chamberlin 1948: Fig. 82

Under Article 13(a) of I.C.Z.N. Rules this name is a nomen nudum. The material is easily recognized, however, and both sexes are present in the AMNH Collection. It is most certainly not a *Spirembolus*.

Tortembolus approximatus Chamberlin 1948:557

This is an easily recognized species, which does not belong in *Spirembolus*.

Species Descriptions—These are given in the order shown in Table 1. All figures of palps are of the right palp.

Distribution and Natural History.—The genus *Spirembolus* is limited to western North America, with records from Mexico to Alaska; the most easterly record is in Colorado (longitude 104° W). The majority of the records are from California, possibly only because this has been a popular area for collecting: of the 38 species described, 30 are

Table 1.—Genus *Spirembolus*: list of species. The species are described in the text in the order given. For definitions of the species groups see text.

monticolens species group

- S. monticolens* (Chamberlin)
- S. pachygnathus* Chamberlin and Ivie
- S. prominens*, new species
- S. pallidus* Chamberlin and Ivie
- S. maderus* Chamberlin

spirotubus species group

- S. spirotubus* (Banks)
- S. vallicolens* Chamberlin
- S. synopticus* Crosby
- S. proximus*, new species
- S. montivagus*, new species
- S. phylax* Chamberlin and Ivie
- S. perjucundus* Crosby
- S. humilis*, new species
- S. mendax*, new species
- S. hibernus*, new species
- S. falcatus*, new species
- S. tiogensis*, new species
- S. whitneyanus* Chamberlin and Ivie
- S. venustus*, new species
- S. chilkatensis* (Chamberlin and Ivie), new combination
- S. mundus* Chamberlin and Ivie
- S. latebricola*, new species
- S. elevatus*, new species
- S. dispar*, new species
- S. abnormis*, new species

tortuosus species group

- S. tortuosus* (Crosby), new combination
 - S. fuscus*, new species
 - S. demonologicus* (Crosby), new combination
 - S. pusillus*, new species
 - S. levis*, new species
 - S. fasciatus* (Banks), new combination
 - S. novellus*, new species
 - S. erratus*, new species
 - S. monicus* (Chamberlin), new combination
 - S. praelongus*, new species
 - S. bilobatus* (Chamberlin and Ivie), new combination
 - S. redondo* (Chamberlin and Ivie), new combination
 - S. mirus*, new species
-

known to be present in California. When other western States have been equally well worked, there is little doubt that additional new species will be discovered.

Information on the natural history of the *Spirembolus* species is sparse indeed: only in very rare instances is any indication of the type of habitat to be found on the vial labels or in previous publications. It seems probable that, like most erigonines, the species are ground living, but may occasionally be found on low herbage.

Keys to Species.—Partial keys have been drawn up for the species (Tables 2 and 3). With genera like *Spirembolus*, where there are numerous species exhibiting rather small structural differences, purely dichotomous keys are not only difficult to draw up and tiresome to use, but are likely in unskilled hands or if used uncritically to lead to false identifications. In the author's view, it is preferable in such cases to have partial keys in which the reader is directed, by a tabular presentation, to groups of species which share one or more characters; after which, for final identification, it is necessary (in most cases) to refer to the species descriptions. It is practically certain that further new species of *Spirembolus* will be collected, and these are more likely to be recognized as such when a partial key of this kind is used for diagnosis.

Spirembolus monticolens (Chamberlin)

Figures 1,2,3,7,9,11,13,15,17; Map 1

Cornicularia monticolens Chamberlin 1919: 251

Spirembolus monticolens: Chamberlin 1920: 197; Crosby 1925: 113; Chamberlin and Ivie 1933: 18, 1945: 217; Roewer 1942: 665; Bonnet 1958: 4122

Holotype.—Male holotype from Chalk Creek, Uintah Mts., Utah, August 1917 (R. V. Chamberlin); in MCZ, examined.

Description.—Total length: female 1.7-1.9 mm, male 1.6-1.7 mm. Carapace: Length: female 0.80 mm, male 0.70-0.75 mm. Chestnut brown with dusky markings and margins. Male carapace raised anteriorly and projecting over clypeus (Figs. 9, 13). Chelicerae: rather swollen anteriorly in male (Fig. 13). Abdomen: grey to black. Sternum: orange-brown, suffused with black. Legs: brown. Tibial spines: female 2221, male 0011; TmI: female 0.47-0.50, male 0.45-0.47. Male palp: Figs. 1,2,3,7. Female palp: tibia with 2 trichobothria (Fig. 15). Epigynum: Figs. 11, 17; the posterior plate is relatively broader than in most other species.

Diagnosis.—In the male, the carapace shape (Fig. 9), coupled with the form of the palpal tibia (Fig. 7), distinguish this species from all others except *S. pachygnathus* and *S. prominens*. From these two latter species, *S. monticolens* is separated by the diameter of the embolic coil, which is smaller in *S. pachygnathus* and larger in *S. prominens* (Fig. 1 cf. Figs. 4, 6). In the female, the epigynum distinguishes *S. monticolens* (with *S. pachygnathus* and *S. prominens*) from the other species which have two trichobothria on the palpal tibia. *S. monticolens* female is separated from *S. pachygnathus* by the internal genitalia (Fig. 17 cf. Fig. 20); these two species are usually separable also by the presence in *S. pachygnathus* of three trichobothria on the right palpal tibia. *S. monticolens* is distinguished from *S. prominens* by the genitalia, the ducts in the latter species being stouter and with a different configuration (Fig. 17 cf. Fig. 22); these two species may also be separable by the epigyna, the internal ducts being more visible through the integument in *S. prominens* (Fig. 11 cf. Fig. 12).

Table 2.—Partial key to *Spirembolus* species: males. A decision on species identity should be made only after reference to the species descriptions and diagnoses.

-
1. Carapace raised anteriorly into two lobes (Figs. 178, 179)
 - S. bilobatus*, *S. redondo*
 2. Carapace raised into small lobe (Fig. 191)
 - S. mirus*
 3. Carapace raised into distinct lobe (Figs. 138, 163), with hole behind lateral eyes
 - a. Abdomen unicolorous
 - i. Epigastric plates smooth
 - S. tortuosus*
 - ii. Epigastric plates striated
 - S. demonologicus*, *S. monicus* (separation by form of carapace and palps)
 - b. Abdomen with clear pattern of white bars/chevrons
 - i. Epigastric plates smooth
 - S. levis*, *S. fasciatus* (separation by form of carapace and palps)
 - ii. Epigastric plates striated
 - S. pusillus*, *S. novellus*, *S. erratus*, *S. praelongus* (separation by form of carapace and palps)
 4. Carapace raised anteriorly, to a greater or lesser degree, but not into distinct lobe (e.g. Figs. 13, 66, 67): see Sections 5-7
 5. TmI 0.60-0.80. Palpal tibia with 3 trichobothria (Fig. 38)
 - S. mundus*, *S. latebricola*, *S. elevatus*, *S. dispar*, *S. abnormis* (separation by form of carapace, palpal tibia, palpal organs, color and value of TmI)
 6. TmI 0.5 or less. Palpal tibia with 2 trichobothria (Fig. 15), and lacking inferior apophysis
 - a. Male carapace projecting anteriorly (Figs. 9, 13)
 - S. monticolens*, *S. pachygnathus*, *S. prominens* (separation by palpal organs)
 - b. Male carapace not projecting anteriorly (Fig. 28)
 - S. pallidus*, *S. maderus* (separation by palpal organs)
 7. TmI 0.5 or less. Palpal tibia with 3 trichobothria (Fig. 38) and usually with inferior apophysis (e.g. Fig. 30)
 - a. Carapace steeply raised anteriorly (Figs. 66, 68)
 - S. perjucundus*, *S. mendax* (separation by palpal organs)
 - b. Carapace less steeply raised
 - i. Palpal organs with small short coil (Fig. 95)
 - S. whitneyanus*
 - ii. Palpal tibia of general form shown in Fig. 30; palp with white excrescence between femur and patella
 - S. spirotubus*, *S. vallicolens*, *S. synopticus*, *S. proximus*, *S. montivagus* (closely related species: for separation, see species descriptions and diagnoses)
 - iii. Palpal tibia as in Figs. 86, 92, but without white excrescence between femur and patella
 - S. falcatus*, *S. tiogensis* (for separation, see species descriptions and diagnoses)
 - iv. Palpal tibia as in Figs. 64, 81
 - S. humilis*, *S. hibernus* (for separation, see species descriptions and diagnoses)
 - v. Palpal tibia lacking inferior apophysis (Fig. 54)
 - S. phylax*
-

Table 3.—Partial key to *Spirembolus* species: females. A decision on species identity should be made only after reference to the species descriptions and diagnoses.

-
1. Abdomen dorsally with well defined white bars/chevrons
 - a. Epigastric plates with striae (sometimes rather weak)

S. pusillus, *S. novellus*, *S. erratus* (some specimens), *S. praelongus* (for separation, see species descriptions and diagnoses)
 - b. Epigastric plates smooth

S. fuscus, *S. levis*, *S. fasciatus*, *S. erratus* (most specimens) (for separation, see species descriptions and diagnoses)
 2. Abdomen unicolorous: see Sections 3-7
 3. Epigastric plates striated

S. demonologicus, *S. monicus* (separation by epigyna: see species descriptions and diagnoses)
 4. Tibial spines 1111. TmI ca. 0.55

S. bilobatus
 5. Tibial spines 2221. TmI ca. 0.60-0.80

S. mundus, *S. latebricola*, *S. dispar*, *S. abnormis* (separation by size, color, epigyna and value of TmI: see species descriptions and diagnoses)
 6. Tibial spines 2221. TmI 0.5 or less. Palpal tibia with 2 trichobothria (Fig. 15). Note: *S. pachygnathus* has 2 trichobothria on left palpal tibia but usually 3 on right
 - a. Dark colored spiders; epigynum of form shown in Fig. 11

S. monticolens, *S. pachygnathus*, *S. prominens* (for separation, see species descriptions and diagnoses)
 - b. Lighter colored spiders; epigynum of form shown in Figs. 25, 26

S. pallidus, *S. maderus* (for separation, see species descriptions and diagnoses)
 - c. Epigynum of form shown in Fig. 127; small spider, length ca. 1.30-1.40 mm

S. tortuosus
 - d. Epigynum of form shown in Fig. 186

S. redondo (this species sometimes has 3 trichobothria on the palpal tibia: hence see also Section 7 of this Key)
 7. Tibial spines 2221. TmI 0.55 or less. Palpal tibia with 3 trichobothria (Fig. 38), one of which is smaller and sometimes rather inconspicuous
 - a. Epigynum Fig. 52

S. proximus
 - b. Epigynum Fig. 98

S. venustus
 - c. Epigynum Fig. 100

S. chilkatensis
 - d. Epigynum Fig. 93

S. whitneyanus
 - e. Epigynum Fig. 186

S. redondo

The remaining species in this section are less easy to diagnose. The epigyna fall into two groups:

 - f. Epigynum Fig. 31

S. spirotubus, *S. vallicolens*, *S. synopticus*, *S. montivagus* (for separation, see species descriptions and diagnoses)
 - g. Epigyna Figs. 56, 69, 70, 71, 72, 79, 82, 88

S. phylax, *S. perjucundus*, *S. humilis*, *S. mendax*, *S. hibernus*, *S. falcatus* (for separation, see species descriptions and diagnoses)
-

Distribution.—*S. monticolens* is one of the most widely distributed of the *Spirembolus* species; it has been recorded from Utah, Wyoming, Nevada, Idaho, California, Oregon, Washington and British Columbia (Map 1).

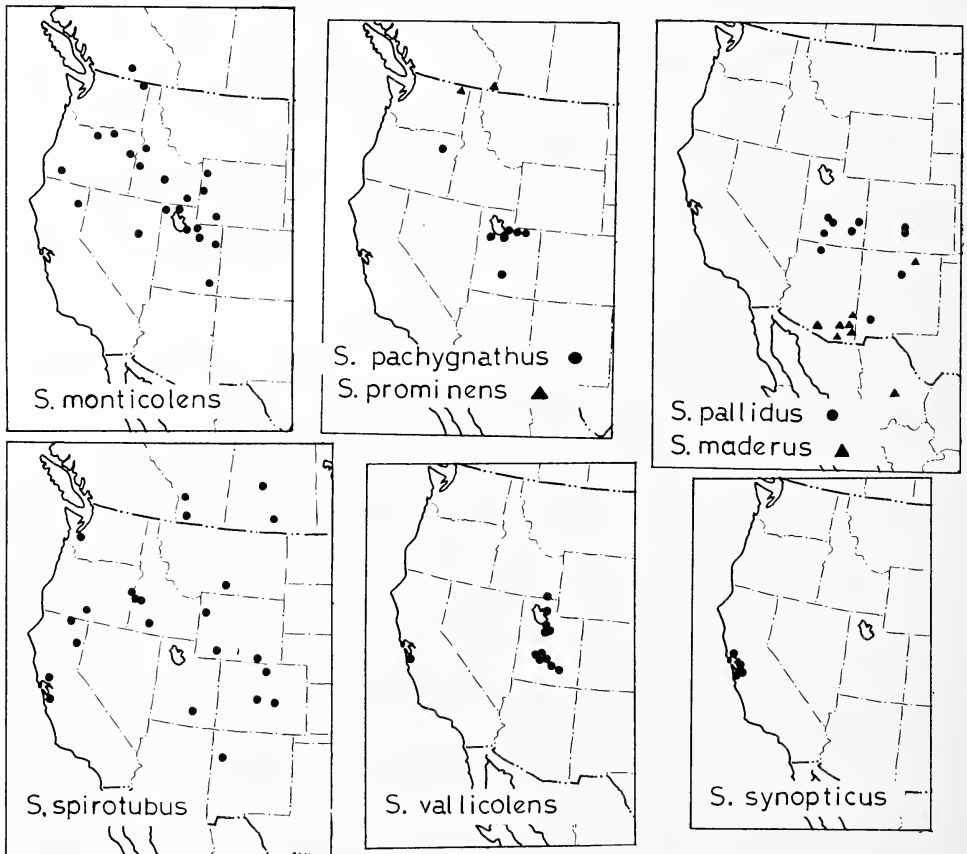
Natural History.—Males and females have been taken in April, May, June, July, August, September, October and November. The main maturity period would seem to be in summer. The only habitat recorded is among dead leaves.

Spirembolus pachygnathus Chamberlin and Ivie
Figures 4, 5, 16, 20; Map 1

Spirembolus pachygnathus Chamberlin and Ivie 1935: 18, 1945: 218; Roewer 1942: 666; Bonnet 1958: 4123

Holotype.—Male holotype from Fish Lake, Sevier County, Utah, September 4, 1929 (R. V. Chamberlin); in AMNH, examined.

Description.—Total length: female 1.9-2.1 mm, male 1.7-1.8 mm. Carapace: length: female/male 0.90 mm. Apart from its slightly larger size, this species closely resembles *S.*

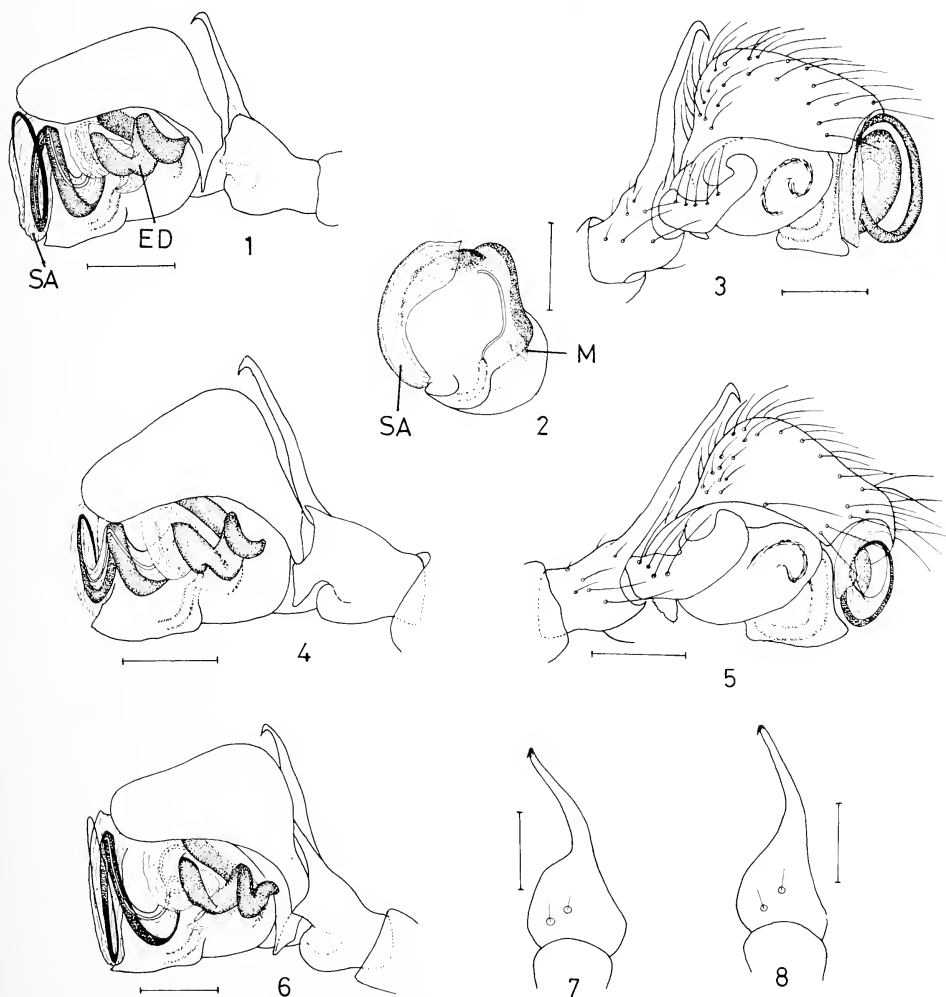


Map 1.—Western North America: distributions of *S. monticolens*, *S. pachygnathus*, *S. prominens*, *S. pallidus*, *S. maderus*, *S. spirotubus*, *S. vallicolens* and *S. synopticus*.

monticolens. Male palp: Figs. 4, 5; the embolic coil is relatively small in diameter. Female palp: the left palpal tibia usually has 2 trichobothria while the right has 3. Epigynum: not distinguishable from that of *S. monticolens*. Internal genitalia Fig. 20.

Diagnosis.—The male of this species is readily separated from *S. monticolens* and *S. prominens* by the smaller diameter of the embolic coil (Fig. 4 cf. Fig. 1). The female is distinguished from *S. monticolens* and from *S. prominens* by the internal genitalia (Fig. 20 cf. Figs. 17, 22) and usually also by the trichobothria on the palpal tibiae. Females taken without males should always be identified with caution, however.

Distribution.—This species is much less widely distributed than *S. monticolens*, with records from Utah and Oregon only (Map 1).



Figs. 1-8.—1, *S. monticolens*, male palp, mesal; 2, *S. monticolens*, male palpal organ, antero-mesal, ED removed; 3, *S. monticolens*, male palp, ectal; 4, *S. pachygnathus*, male palp, mesal; 5, *S. pachygnathus*, male palp, ectal; 6, *S. prominens*, male palp, mesal; 7, *S. monticolens*, male palpal tibia, dorsal; 8, *S. prominens*, male palpal tibia, dorsal. Abbreviations: ED, embolic division; M, membranous apophysis; SA, suprategular apophysis (Scale lines 0.1 mm).

Natural History.—Males have been recorded in March, April, June, August and September, females in February, April, June, August and September. Nothing is known on habitat.

Spirembolus prominens, new species

Figures 6, 8, 10, 12, 14, 22; Map 1

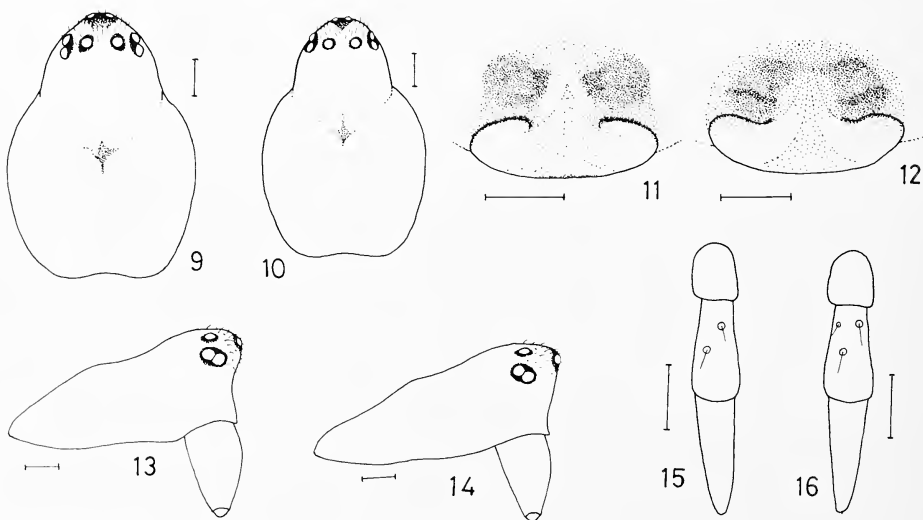
Holotype.—Male holotype from Cedar Lake, Stevens County, Washington, September 30, 1964 (J. and W. Ivie); deposited in AMNH.

Description.—Total length: female 1.75-1.80 mm, male 1.60 mm. Carapace: length: female 0.75-0.80 mm, male 0.75 mm. Brown, with dusky markings and margins. The male carapace projects anteriorly as in *S. monticolens* (Fig. 10, 14). Chelicerae: rather swollen anteriorly in male. Abdomen: grey to black. Sternum: brown, suffused with black. Legs: brown. Tibial spines: female 2221, male 0211, but weak on legs II. Tml: female 0.42-0.48, male 0.47. Male palp: Figs. 6, 8; the embolus is in a large coil. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 12, 22.

Diagnosis.—This species resembles *S. monticolens* and *S. pachygnathus* in most characters. The male of *S. prominens* is distinguished from these species by the larger diameter of the embolic coil, and by the narrower width of the ribbon-like part of the embolus (Fig. 6 cf. Figs. 1, 4). The female is separated by the epigynum, where the somewhat stouter internal ducts are visible through the integument (Fig. 12 cf. Fig. 11), and by the internal genitalia (Fig. 22 cf. Figs. 17, 20) (see also *S. monticolens* diagnosis).

Distribution.—Known only from Washington (type locality) and from Alberta, Canada (Map 1).

Natural History.—The males were taken in June (Alberta) and September (Washington), and the females in September (Washington). The Alberta specimen was taken in a pitfall trap in an open grassy area in coniferous woods at 1675 m altitude.



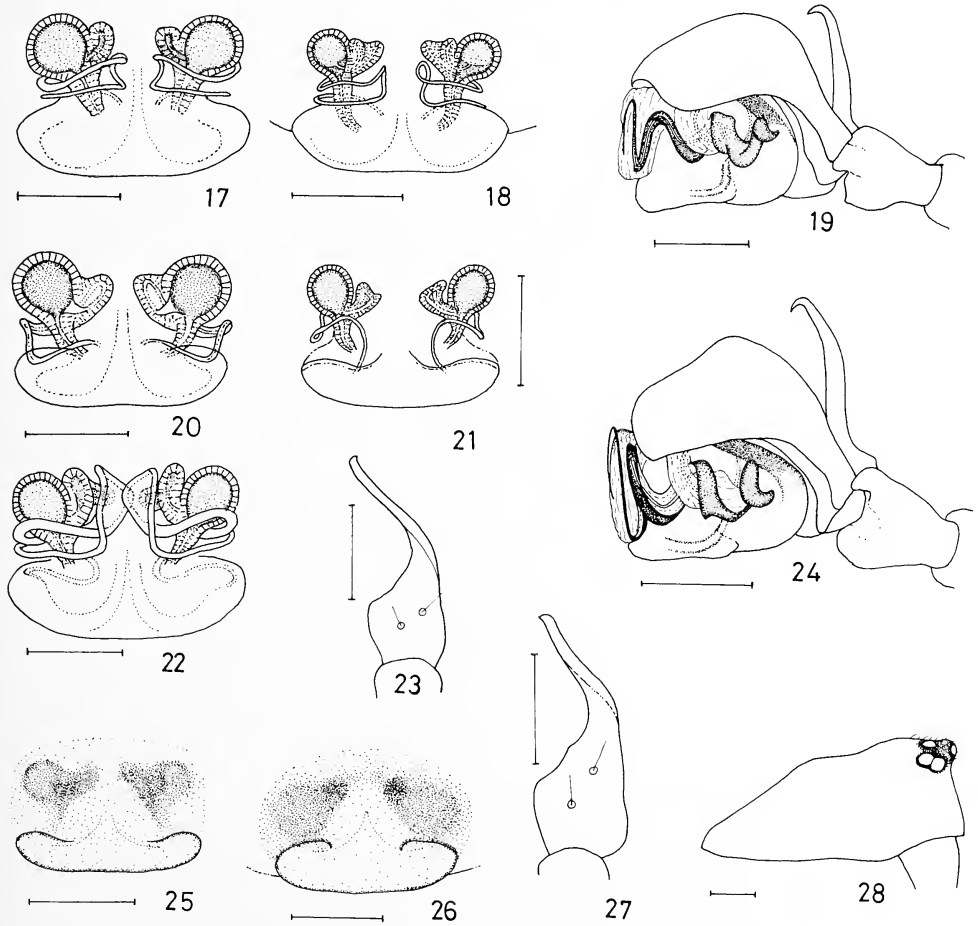
Figs. 9-16.—9, *S. monticolens*, male carapace, dorsal; 10, *S. prominens*, male carapace, dorsal; 11, *S. monticolens*, epigynum; 12, *S. prominens*, epigynum; 13, *S. monticolens*, male carapace, lateral; 14, *S. prominens*, male carapace, lateral; 15, *S. monticolens*, female palpal tibia and tarsus, dorsal; 16, *S. pachygnathus*, right hand female palpal tibia and tarsus, dorsal (Scale lines 0.1 mm).

Spirembolus pallidus Chamberlin and Ivie
Figures 19, 21, 23, 25, 28; Map 1

Spirembolus pallidus Chamberlin and Ivie 1935: 19, 1945: 223; Roewer 1942: 666; Bonnet 1958: 4123

Holotype.—Male holotype from Mount Ellen, Henry Mountains, Utah, September 11, 1929 (R. V. Chamberlin); in AMNH, examined.

Description.—Total length: female 1.55-1.65 mm, male 1.45-1.55 mm. Carapace: length: female 0.65 mm, male 0.60 mm. Pale brown to brown with faint dusky markings. Male carapace only slightly raised anteriorly (Fig. 28); the anterior median eyes are borne on a small prominence. Abdomen: whitish grey to grey, clothed with short hairs. Sternum: yellow to pale brown, darker on margins. Legs: pale brown to brown. Tibial



Figs. 17-28.—17, *S. monticolens*, internal genitalia, ventral; 18, *S. maderus*, internal genitalia, ventral; 19, *S. pallidus*, male palp, mesal; 20, *S. pachygnathus*, internal genitalia, ventral; 21, *S. pallidus*, internal genitalia, ventral; 22, *S. prominens*, internal genitalia, ventral; 23, *S. pallidus*, male palpal tibia, dorsal; 24, *S. maderus*, male palp, mesal; 25, *S. pallidus*, epigynum; 26, *S. maderus*, epigynum; 27, *S. maderus*, male palpal tibia, dorsal; 28, *S. pallidus*, male carapace, lateral (Scale lines 0.1 mm).

spines: female 2221, male 1121 but short and weak. TmI: female 0.35-0.40, male 0.35. Male palp: Figs. 19, 23; the embolus forms a rather small coil. The tibia is similar in general form to that of *S. monticolens*. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 25, 21.

Diagnosis.—*S. pallidus* is one of the small group of species which have a unicolorous abdomen and two trichobothria on the palpal tibia. The male is separated clearly from *S. monticolens*, *S. pachygnathus* and *S. prominens* by its relatively pale colour, the form of the male carapace and the form of the palpal tibia (Fig. 23 cf. Figs. 7, 8). From the closely related species *S. maderus*, the male of *S. pallidus* is distinguished by the smaller diameter of the embolic coil (Fig. 19 cf. Fig. 24). The female of *S. pallidus* is separated from the other species in the group (except *S. maderus*) by its pale colour and the epigynum. The epigyna of *S. pallidus* and *S. maderus* though very similar are usually distinct (Fig. 25 cf. Fig. 26), but occasionally they may be difficult to distinguish. Supporting evidence is offered by the relatively stouter legs of *S. pallidus*, which has e.g. tibia I 1/d ca. 4, MTI 1/d ca. 6, cf. corresponding figures for *S. maderus* of 5 and 7. *S. pallidus* is normally (but probably not invariably) paler in color than *S. maderus*.

Distribution.—*S. pallidus* has been found so far only in Utah, Colorado and New Mexico (Map 1).

Natural History.—Males have been taken in April and September, females in April, May, July, September and October. There is no information on habitat.

Spirembolus maderus Chamberlin

Figures 18, 24, 26, 27; Map 1

Spirembolus maderus Chamberlin 1948: 547

Types.—Female holotype from Madera Canyon, Santa Rita Mts., Arizona, September 8, 1941 (W. Ivie); in AMNH, examined. The two "paratypes" from California mentioned by Chamberlin (1948) were found to be *S. hibernus*.

Description.—The male, which was taken with the female, is described for the first time. Total length: female 1.7-1.8 mm, male 1.45 mm. Carapace: length: female 0.80 mm, male 0.65 mm. Brown, with dusky markings and margins. Male carapace as in *S. pallidus*. Abdomen: grey to black. Sternum: brown suffused with black. Legs: brown. Tibial spines: female and male 2221, but spines much weaker in male. TmI: female 0.40-0.44, male 0.40. Male palp: Figs. 24, 27; very similar to that of *S. pallidus*, but the embolic coil is larger in diameter. Female palp: tibia with 2 trichobothria. Epigynum: Fig. 26; somewhat variable, and sometimes rather close to that of *S. pallidus*. The internal genitalia (Fig. 18) show the same differences from those of *S. pallidus* as is the case with *S. monticolens* / *S. pachygnathus*.

Diagnosis.—*S. maderus* is close to *S. pallidus* (q.v.). The males are distinguishable by the diameters of the embolic coil (Fig. 24 cf. Fig. 19). The separation of the females can be more difficult; the epigyna are usually sufficiently distinctive (Fig. 26 cf. Fig. 25), but occasionally the differences are less clear. The legs of *S. maderus* female are slightly less stout than those of *S. pallidus* (q.v.), and this can be used to check the identity of doubtful specimens. *S. maderus* is usually somewhat darker in color than *S. pallidus*.

Distribution.—This species has been taken in Arizona, New Mexico and Mexico, mostly at altitudes well above sea level (Map 1).

Natural History.—Males have been taken in May, June and July, females in May, June, July, August, September, October and December (Mexico). The chief period of maturity seems to be in summer. Nothing is recorded on habitat.

Spirembolus spirotubus (Banks)

Figures 29,30,31,32,33,35,36,38,42; Map 1

Tiso spirotubus Banks 1895: 424.

Spirembolus spirotubus: Crosby 1925: 113; Roewer 1942: 666; Chamberlin and Ivie 1945: 221

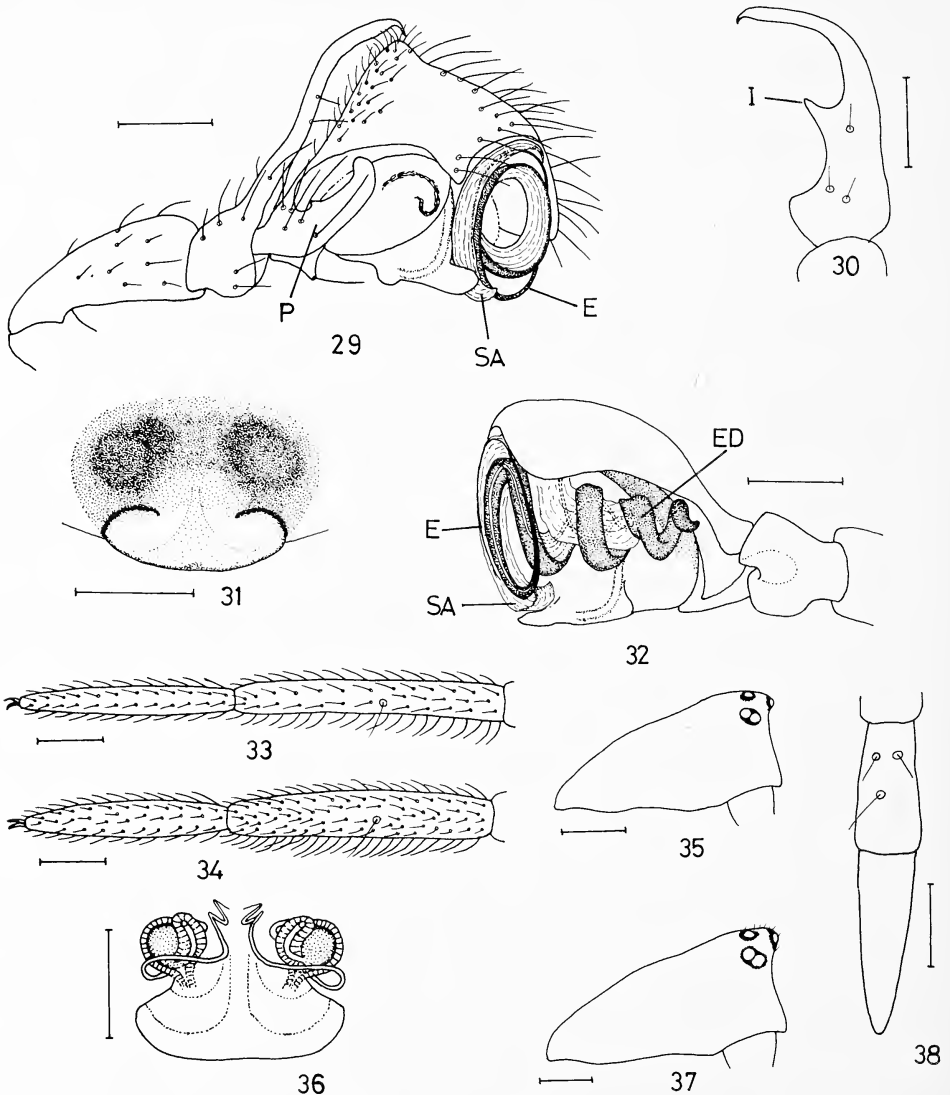
Spirembolus spiritubus: Bonnet 1958: 4123

Types.—Three males from Fort Collins, Colorado; in MCZ, examined.

Description.—Total length: female 1.9-2.0 mm, male 1.60-1.70 mm. Carapace: length: female 0.9 mm, male 0.75 mm. Deep brown, with dusky markings and margins. Male carapace smoothly elevated anteriorly, with clypeus not very concave (Fig. 35). Abdomen: black to grey. Sternum: deep brown to orange brown, suffused with black. Legs: brown. Tibial spines: female 2221, male 0021. Tml: female 0.48-0.55, male 0.44-0.46. The metatarsi and tarsi of legs I of the male are less fusiform and have fewer hairs than in *S. vallicolens* (Fig. 33). Male palp: Figs. 29, 30, 32, 42. There is a distinct white excrescence, of rather variable size, on the joint between femur and patella: Crosby (1925) was mistaken in his statement, in his key, that the excrescence is absent in *S. spirotubus*. Female palp: tibia with three trichobothria (Fig. 38). Epigynum: Figs. 31, 36: the posterior plate is usually greyish white in color, and the spermathecae are indistinctly visible through the dark colored integument. The female genitalia, palpal organs and palpal tibiae of specimens taken at the limits of its known range (New Mexico and Canada) show no more than minimal variations.

Diagnosis.—This species falls into Section 7 in the Keys. The male of *S. spirotubus* is grouped with the closely related species *S. vallicolens*, *S. synopticus*, *S. proximus* and *S. montivagus* by the form of the palpal tibia coupled with the presence of the white excrescence between the palpal femur and patella. From *S. vallicolens* the male of *S. spirotubus* is distinguishable only by the small differences in the metatarsi and tarsi of legs I, which in *S. vallicolens* are more fusiform and have more numerous but shorter hairs (Fig. 33 cf. Fig. 34). *S. spirotubus* male is very close to *S. synopticus*, and the two species need to be separated with care. *S. spirotubus* has the embolic coil smaller in diameter and the suprategular apophysis rather shorter (Fig. 42 cf. Fig. 45); the palpal tibiae of the two species also show small differences (Fig. 30 cf. Fig. 31). The profile of the carapace/clypeus (Figs. 35, 37), used by Crosby (1925) to separate *S. spirotubus* and *S. synopticus*, shows some variation and should be used with caution in diagnosis. *S. spirotubus* male is distinguished from *S. proximus* by the presence in the latter of striated epigastric plates, and of a relatively much longer palpal patella (Fig. 29 cf. Fig. 48). The males of *S. spirotubus* and *S. montivagus* can be separated only by a small difference in the palpal tibiae (Fig. 30 cf. Fig. 43). In the female sex, *S. spirotubus* is grouped with *S. vallicolens*, *S. synopticus*, and *S. montivagus* by the epigynum, which is usually rather dark in color and obscure in pattern. The females of *S. spirotubus* and *S. vallicolens* cannot be separated by structural characters; the distribution of these two species appears on the whole to be different, however, and when further information has been obtained on distribution and/or habitat, females of the two species may perhaps be separable by ecological rather

than structural considerations. The epigyna of *S. spirotubus* and *S. synopticus* seem not to be distinguishable, and the internal genitalia are also very close; there is a small difference in the relative stoutness of the legs: e.g. tibia I/d in *S. spirotubus* female is ca. 5, in *S. synopticus* ca. 6. *S. spirotubus* and *S. montivagus* are likewise indistinguishable by their epigyna, but there are small though distinct differences in the internal genitalia (Fig. 36 cf. Fig. 37). *S. montivagus* may also be distinguishable from *S. spirotubus* by its ecology, being probably a very high altitude species.



Figs. 29-38.—29, *S. spirotubus*, male palp, ectal; 30, *S. spirotubus*, male palpal tibia, dorsal; 31, *S. spirotubus*, epigynum; 32, *S. spirotubus*, male palp, mesal; 33, *S. spirotubus*, male metatarsus and tarsus, leg I, dorsal; 34, *S. vallicolens*, male metatarsus and tarsus, leg I, dorsal; 35, *S. spirotubus*, male carapace, lateral; 36, *S. spirotubus*, internal genitalia, ventral; 37, *S. synopticus*, male carapace, lateral; 38, *S. spirotubus*, female palpal tibia and tarsus, dorsal. Abbreviations: E, embolus; I, inferior tibial apophysis; P, paracymbium; SA, suprategular apophysis; TP, tailpiece (Scale lines 0.1 mm, except Figs. 35, 37, 0.2 mm).

Distribution.—This is the most widely distributed of the *Spirembolus* species, with records from New Mexico in the south to Canada in the north. There is only one record from Utah, but at this locality (Mt. Ellen, Henry Mts.: September 1929) *S. spirotubus* was sympatric with the closely related *S. vallicolens*. Because of the impossibility of distinguishing isolated females of *S. spirotubus* and *S. vallicolens*, only those localities where a male was taken are given in Map 1.

Natural History.—Adults of both sexes have been taken in practically every month of the year, but they seem to be most numerous in June–September. The species has been obtained by sweeping meadows (in Wyoming) and in pitfall traps in grassland and marshy ground in Alberta and Saskatchewan (Canada).

S. vallicolens (Chamberlin)

Figures 34, 46; Map 1

Cornicularia vallicolens Chamberlin 1920: 198.

Spirembolus vallicolens: Crosby 1925: 112; Roewer 1942: 666; Chamberlin and Ivie 1945: 220 (in part only); Bonnet 1958: 4123

Holotype.—Male holotype from Mill Creek Canyon, Utah, September 1929 (R. V. Chamberlin); in MCZ, examined.

Description.—In color, size and chaetotaxy this species is practically identical with *S. spirotubus*. The sex organs are also identical with those of *S. spirotubus*. The metatarsi and tarsi of legs I of the male are distinctly fusiform (Fig. 34), and fairly densely clothed with short hairs (cf. *S. spirotubus* Fig. 33); this small difference between the two species is clear and recognizable in preserved specimens.

S. vallicolens and *S. spirotubus* were confused by Chamberlin and Ivie (1945), and many of the vials in AMNH labelled "*S. vallicolens*" are in fact *S. spirotubus*. It is possible that *S. vallicolens* should be regarded as a sub-species of *S. spirotubus*; against this is the fact that the two species were sympatric in one locality (see *S. spirotubus*) and that no intermediates between the two forms have been seen.

Diagnosis.—*S. vallicolens* is very close to *S. spirotubus*, and its diagnosis is dealt with under that species.

Distribution.—Many of the records given by Chamberlin and Ivie (1945) refer to *S. spirotubus*. The majority of the true records are from Utah, with one from Idaho and one from California; the localities shown (Map 1) are limited to those where the male has been taken. In view of the apparently rather limited distribution, the California record (Palo Alto: J. C. Chamberlin, 1920–1921) needs confirmation.

Natural History.—Adults of both sexes have occurred throughout the year. There is no information on habitat.

Spirembolus synopticus Crosby in Chamberlin 1925

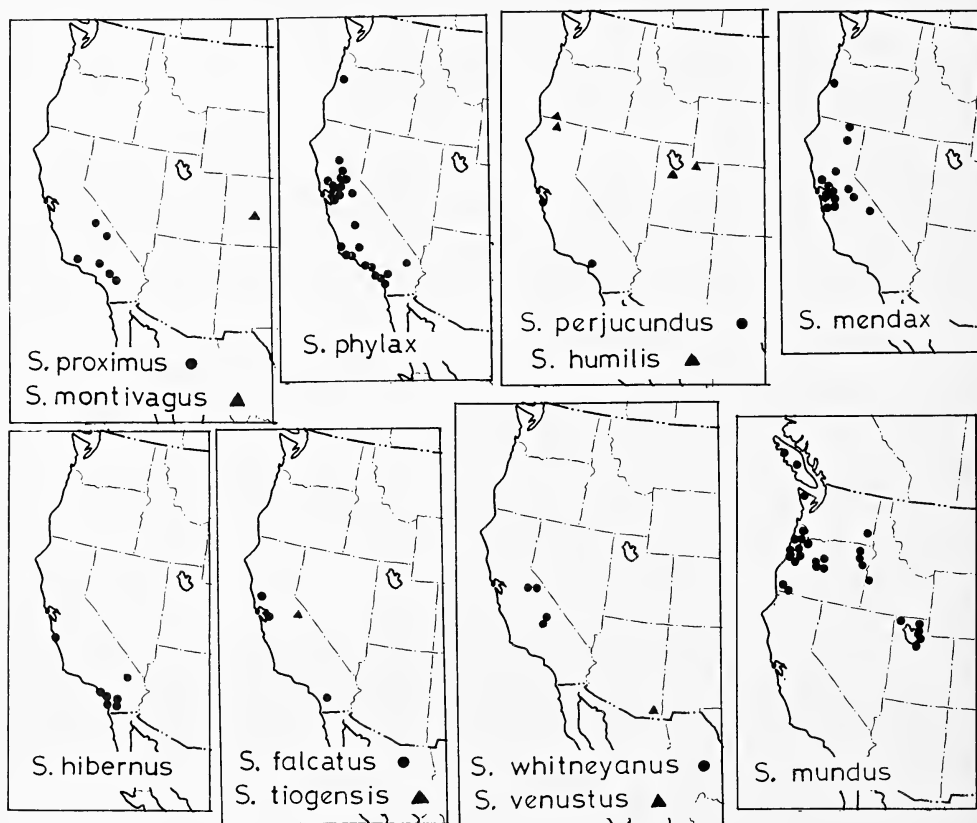
Figures 37, 39, 40, 41, 45, 49; Map 1

Spirembolus synopticus Crosby in Chamberlin 1925: 113; Roewer 1942: 666; Chamberlin and Ivie 1945: 219; Bonnet 1958: 4123

Holotype.—Male holotype from Berkeley, California, November 1919 (H. Dietrich); in MCZ, examine.

Description.—The female, described here for the first time, was not taken with the male, and its identity must be regarded as not completely certain; it agrees in most characters, however, with the male. Total length: female 2.1 mm, male 1.9-2.15 mm. Carapace: length: female 0.95 mm, male 0.90-1.0 mm. Deep brown, with blackish markings and margins. Male carapace only moderately raised, with clypeus fairly concave (Fig. 37). Abdomen: black. Sternum: deep brown, heavily suffused with black. Legs: yellow-brown to orange-brown. Tibial spines: female, spines missing, male 0021. Tml: female 0.51, male 0.50-0.55. Male palp: Figs. 41, 45, 49. There is a conspicuous white excrescence on the joint between femur and patella, particularly pronounced on the mesal side (Fig. 40). Female palp: tibia with 3 trichobothria. Epigynum: not distinguishable from that of *S. spirotubus*. Internal genitalia: Fig. 39.

Diagnosis.—*S. synopticus* is closely related to *S. spirotubus*, *S. vallicolens*, *S. proximus* and *S. montivagus*. Separation from *S. spirotubus*/*S. vallicolens* is dealt with under *S. spirotubus*. Females of *S. synopticus* and *S. proximus* can be distinguished by the epigyna; the males are separable by the greater length of the palpal patella in *S. proximus* (Fig. 49 cf. Fig. 48), by the presence in *S. proximus* in most cases of clear striae on the epigastric plates, and by the less steeply raised carapace of *S. synopticus* (Fig. 37 cf. Fig. 51). There are also small differences in the stoutness of the legs, tibia I 1/d for *S.*

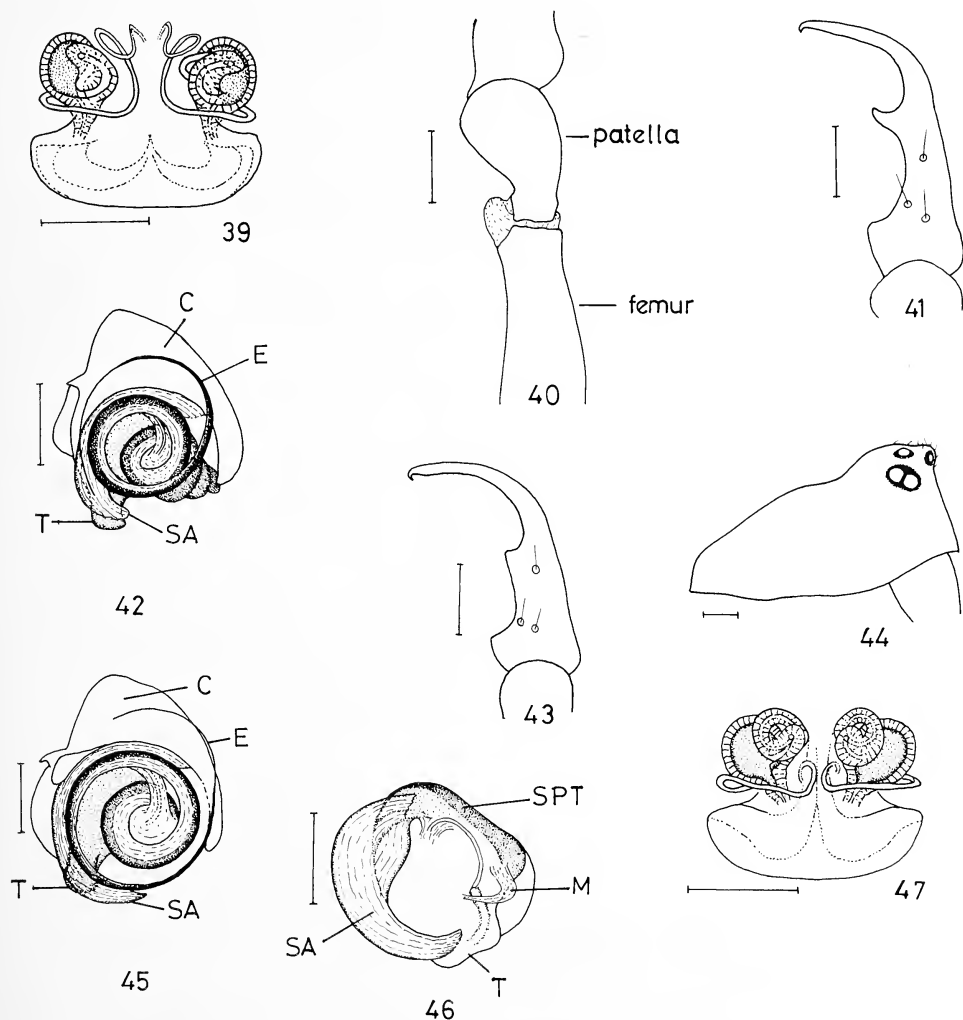


Map 2.—Western North America: distributions of *S. proximus*, *S. montivagus*, *S. phylax*, *S. perjucundus*, *S. humilis*, *S. mendax*, *S. hibernus*, *S. falcatus*, *S. tiogensis*, *S. whitneyanus*, *S. venustus* and *S. mundus*.

synopticus being 6 (female), 6-6.5 (male), and for *S. proximus* 7 (female), 8 (male). From *S. montivagus*, *S. synopticus* is separated in the male by the form of the palpal tibia (Fig. 41 cf. Fig. 43) and by the form of the carapace (Fig. 37 cf. Fig. 41). The females can be separated only by the internal genitalia (Fig. 39 cf. Fig. 47). *S. synopticus* is probably a low altitude species, while *S. montivagus* is a high mountain species.

Distribution.—Known only from a few localities in California (Map 1).

Natural History.—Males have been taken in autumn, November and December, and the possible female in December. The types were taken by sifting, and from branches of pine.



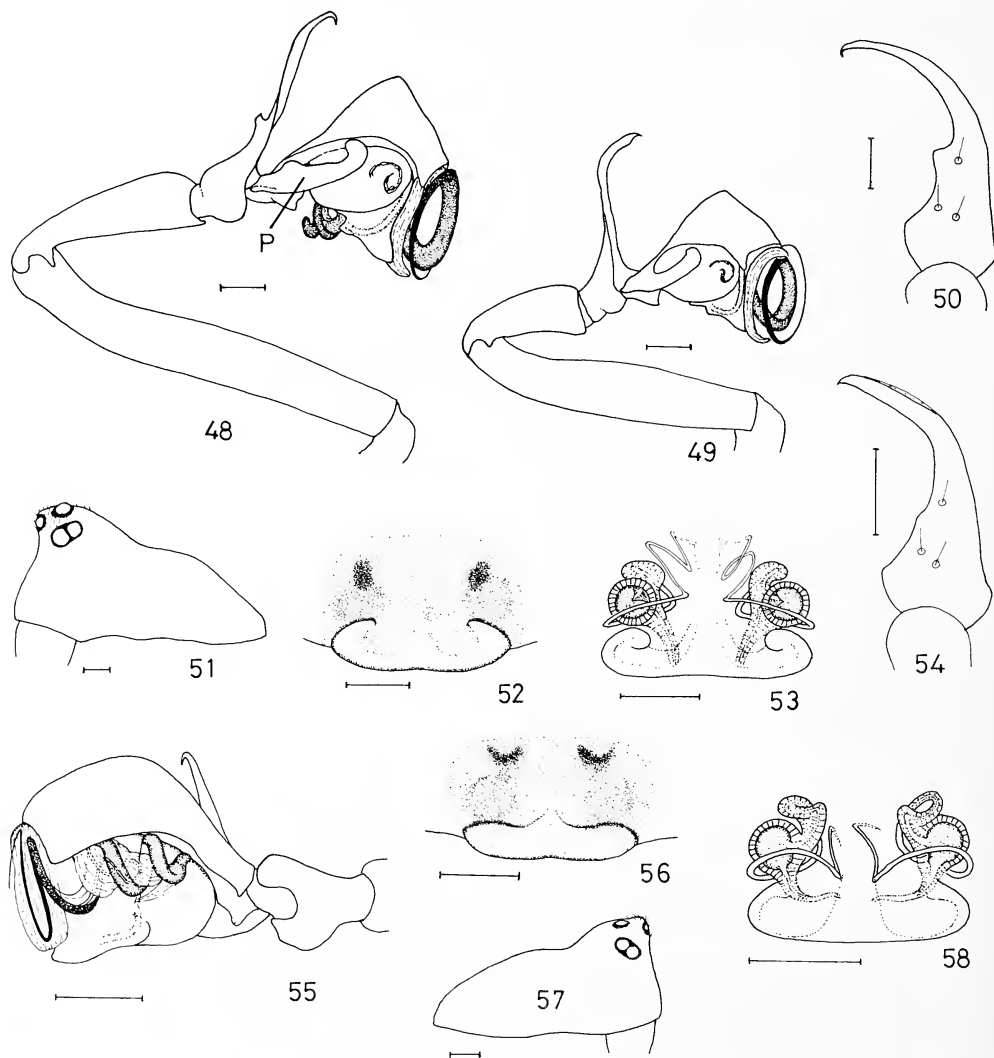
Figs. 39-47.—39, *S. synopticus*, internal genitalia, ventral; 40, *S. synopticus*, male palp, dorsal, showing excrescence between femur and patella; 41, *S. synopticus*, male palpal tibia, dorsal; 42, *S. spirotubus*, male palpal organ, from in front; 43, *S. montivagus*, male palpal tibia, dorsal; 44, *S. montivagus*, male carapace, lateral; 45, *S. synopticus*, male palpal organ, from in front; 46, *S. vallicolens*, male palpal organ, antero-mesal, ED removed; 47, *S. montivagus*, internal genitalia, ventral. Abbreviations: C, cymbium; E, embolus; M, membranous apophysis; SA, supratergular apophysis; SPT, supratergulum; T, tegulum (Scale lines 0.1 mm).

Spirembolus proximus, new species

Figures 48,50,51,52,53; Map 2

Holotype.—Male holotype from Mount Pinos, California, July 31, 1961 (Roth and Roth); deposited in AMNH.

Description.—The female described was not taken with the male, but from its characters it seems probable that it is of the same species. Total length: female 2.85-3.0 mm, male 2.1-2.15 mm. Carapace: length: female 1.2-1.25 mm, male 0.95 mm. Orange-brown to red-brown. Male carapace raised fairly sharply anteriorly (Fig. 51). Abdomen: grey to black. Epigastric plates of male with fairly closely spaced striae, sometimes



Figs. 48-58.—48, *S. proximus*, male palp, lateral; 49, *S. synopticus*, male palp, lateral; 50, *S. proximus*, male palpal tibia, dorsal; 51, *S. proximus*, male carapace, lateral; 52, *S. proximus*, epigynum; 53, *S. proximus*, internal genitalia, ventral; 54, *S. phylax*, male palpal tibia, dorsal; 55, *S. phylax*, male palp, mesal; 56, *S. phylax*, epigynum; 57, *S. phylax*, male carapace, lateral; 58, *S. phylax*, internal genitalia, ventral. Abbreviation: P, paracymbium (Scale lines 0.1 mm).

weakly developed; in the female the striae are closely spaced and very weak or absent. Sternum: orange-brown, suffused with black. Legs: orange-brown, rather long and thin. Tibial spines: female 2221, male 0021. TmI: female 0.45-0.50, male 0.46-0.51. Male palp: Figs. 48, 50; the femur and patella are relatively long. There is a small white excrescence between femur and patella. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 52, 53. The epigynum and internal genitalia are similar to those of *S. mundus*, but the spermathecae are more widely spaced.

Diagnosis.—*S. proximus* is closely related to *S. spirotubus*, *S. vallicolens*, *S. synopticus* and *S. montivagus*. For distinctions from *S. spirotubus*, *S. vallicolens* and *S. synopticus*, refer to those species. The male of *S. proximus* has the palpal tibia very similar to that of *S. montivagus*, but the patella is much longer, *S. montivagus* being like *S. spirotubus* in this respect. The females of *S. proximus* and *S. montivagus* can be separated both by the epigyna and by the internal genitalia (Fig. 53 cf. Fig. 47).

Distribution.—Known from a few localities in California (Map 2).

Natural History.—Males have been taken in July, September and December, females in May and June. Nothing is recorded on habitat.

Spirembolus montivagus, new species

Figures 43, 44, 47; Map 2

Holotype.—Male holotype from North Pole Basin, Elk Mts. (12000 feet), Gunnison Co., Colorado, August 9, 1956 (H. and L. Levi); deposited in MCZ.

Description.—Total length: female 1.90-2.0 mm, male 1.80 mm. Carapace: length: female and male 0.80 mm. Brown with dusky markings and margins. Male carapace only very slightly raised (Fig. 44). Abdomen: grey to black. Sternum: brown, reticulated with black. Legs: brown. Tibial spines: female 2221, male 0021. TmI: female 0.45-0.50, male 0.42. Male palp: this is identical with that of *S. spirotubus* in most respects, but there is a small difference in the tibia (Fig. 43, cf. Fig. 30). There is a small white excrescence between femur and patella. Female palp: tibia with 3 trichobothria. Epigynum: not distinguishable from that of *S. spirotubus*. The internal genitalia (Fig. 47), although of the same pattern as in *S. spirotubus*, show distinct differences which are well outside the range of variation of those of *S. spirotubus*.

Diagnosis.—This species is closely related to *S. spirotubus*, *S. vallicolens*, *S. synopticus* and *S. proximus*, and its diagnosis is dealt with under the diagnoses of those species.

Distribution.—Known only from the type locality (Map 2).

Natural History.—It is to be expected that this species will be found only at high altitudes. The specimens collected contained one adult and one sub-adult male, and several adult females; the chief maturity period is almost certainly in summer.

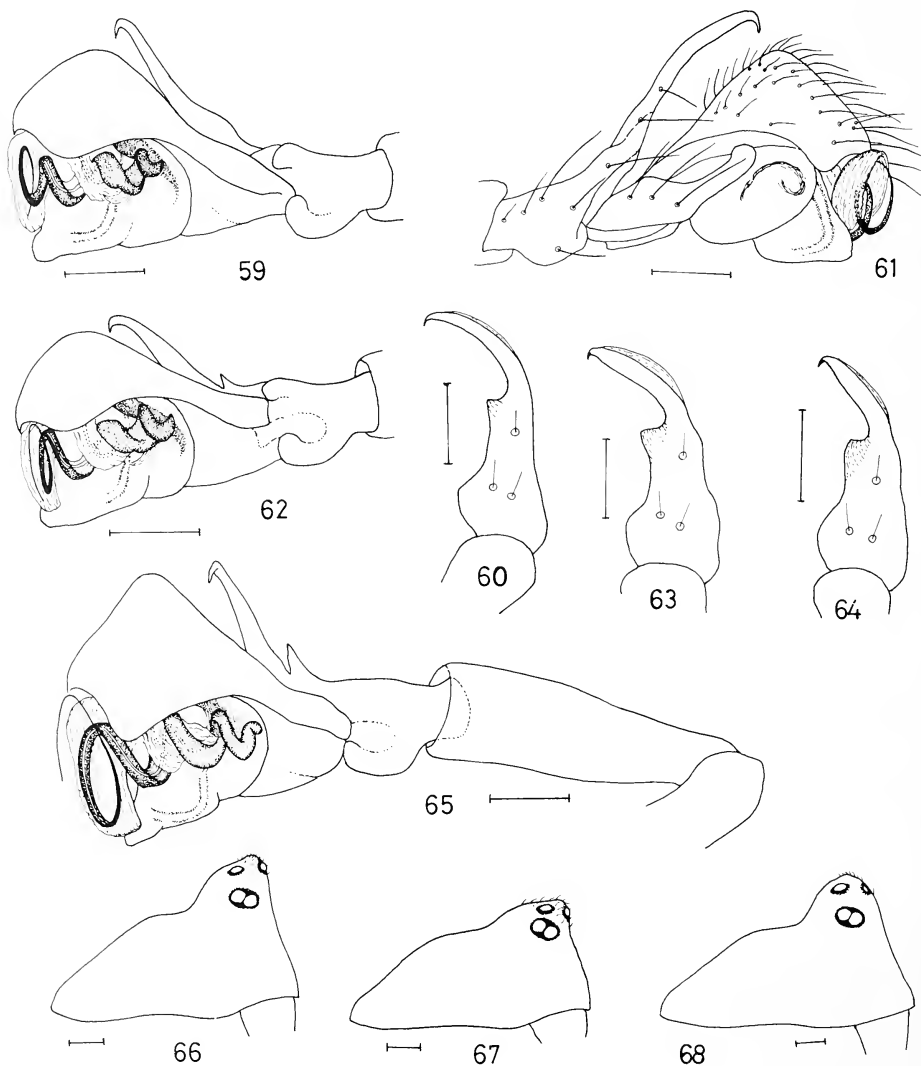
Spirembolus phylax Chamberlin and Ivie

Figures 54, 55, 56, 57, 58; Map 2

Spirembolus phylax Chamberlin and Ivie 1935: 19, 1945: 222; Roewer 1942: 666; Bonnet 1958: 4123

Holotype.—Male holotype from Laguna Beach, California, July 1931 (W. Ivie); in AMNH, examined.

Description.—The female, taken with the male, is described for the first time. Total length: female: 1.7-2.0 mm, male 1.6-1.9 mm. Carapace: length: female and male 0.8 mm. Orange-brown to dark brown, with dusky markings and margins. Male carapace raised sharply anteriorly (Fig. 57). Abdomen: grey to black. Epigastric plates with closely spaced striae in the male, usually absent or extremely weak in the female. Sternum: orange to brown, suffused with some black. Legs: orange-brown. Tibial spines: female 2221, male 0021. TmI: female 0.43-0.48, male 0.40-0.43. Male palp: Figs. 54, 55; the femur is long. The inferior tibial apophysis, the presence of which is characteristic of the



Figs. 59-68.—59, *S. perjucundus*, male palp, mesal; 60, *S. perjucundus*, male palpal tibia, dorsal; 61, *S. perjucundus*, male palp, ectal; 62, *S. humilis*, male palp, mesal; 63, *S. mendax*, male palpal tibia, dorsal; 64, *S. humilis*, male palpal tibia, dorsal; 65, *S. mendax*, male palp, mesal; 66, *S. perjucundus*, male carapace, lateral; 67, *S. humilis*, male carapace, lateral; 68, *S. mendax*, male carapace, lateral (Scale lines 0.1 mm).

spirotubus species group, is absent or vestigial in *S. phylax*. The embolic coil is of medium size. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 56, 58.

Diagnosis.—This species falls into Sections 7 of the Keys. The male of *S. phylax* is distinguished from the others in the Section by the palpal tibia (Fig. 54) which lacks the inferior apophysis; confirmation is given by the form of the carapace (Fig. 57) and by the presence of the striae on the epigastric plates. Diagnosis of the female is based on the epigynum: the two crescent shaped markings are almost always clearly visible anterior to the spermathecae. The epigynum of *S. mendax* can be somewhat similar, but the internal ducts are normally much less visible in *S. phylax* than in *S. mendax* (Fig. 56 cf. Fig. 71, 72); the epigyna of these two species are somewhat variable, however, and the internal genitalia offer a more reliable means of separation (Fig. 58 cf. Fig. 75). The epigynum of *S. phylax* is also quite similar to, but usually distinguishable from, that of *S. falcatus* (Fig. 88); the females of these two species also differ in size (*S. phylax* being larger) and in the stoutness of the legs: metatarsus I 1/d and tibia I 1/d being 8.5-9 and 5.5-6 respectively for *S. phylax* and 7 and 4-4.5 for *S. falcatus*.

Distribution.—Most of the records are from California, with one from Oregon (Map 2).

Natural History.—Both sexes have been taken in practically every month of the year. Nothing is recorded on habitat.

Spirembolus perjucundus Crosby in Chamberlin 1925

Figures 59,60,61,66,69,73; Map 2

Spirembolus perjucundus Crosby in Chamberlin 1925: 114; Roewer 1942: 666; Bonnet 1958: 4123. *Not S. perjucundus* Chamberlin and Ivie 1945: Figs. 28-31.

Types.—Male holotype from San Gregorio Beach, San Mateo Co., California, 1920-1921 (J. C. Chamberlin); in MCZ, examined. The male paratype mentioned by Crosby in the same paper, from Berkeley, California, is *S. elevatus*.

Description.—The female, taken in company with the male, is described for the first time. Total length: female 1.55-1.75 mm, male 1.55-1.60 mm. Carapace: length: female and male 0.70-0.75 mm. Brown to deep brown, with dusky margins. Male carapace sharply raised anteriorly (Fig. 66). Abdomen: grey-black. Sternum: brown, reticulated with black. Legs: brown. Tibial spines: female 2221, male 0021. TmI: female 0.40-0.42, male 0.40. Male palp: Figs. 59, 60, 61. The femur and patella are long; the embolus forms a small coil anteriorly. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 69, 73.

Diagnosis.—The male of *S. perjucundus* is separated from other species in Section 7 of the key, and grouped with *S. mendax*, by the steeply raised carapace (Fig. 66); from *S. mendax*, *S. perjucundus* is readily distinguished by the smaller size of the embolic coil (Fig. 59 cf. Fig. 65). *S. perjucundus* male is very close to *S. humilis*, the chief difference being in the lower anterior elevation of the carapace (Fig. 66 cf. Fig. 67); there are other very small differences: the embolic coil is slightly smaller anteriorly, the SA is slightly shorter and the palpal patella is relatively shorter. The female of *S. perjucundus* is diagnosed by the epigynum, but this is indistinguishable from that of *S. humilis*; the internal genitalia of these two species are also very close and only doubtfully distinguishable. The epigynum of *S. hibernus* is also very similar to that of *S. perjucundus*, but usually distinguishable (Fig. 69 cf. Figs. 79, 82). An additional small difference from *S. hibernus* female lies in the somewhat stouter legs of *S. perjucundus*, where e.g. metatarsus I 1/d is 6-6.5, tibia I 1/d is 4.5, cf. figures of 7.5-8 and 5.5 for *S. hibernus*.

Distribution.—Known only from two localities in California (Map 2).

Natural History.—Males have been taken in April and September, females in September. The only information on habitat is that the holotype was taken on a beach.

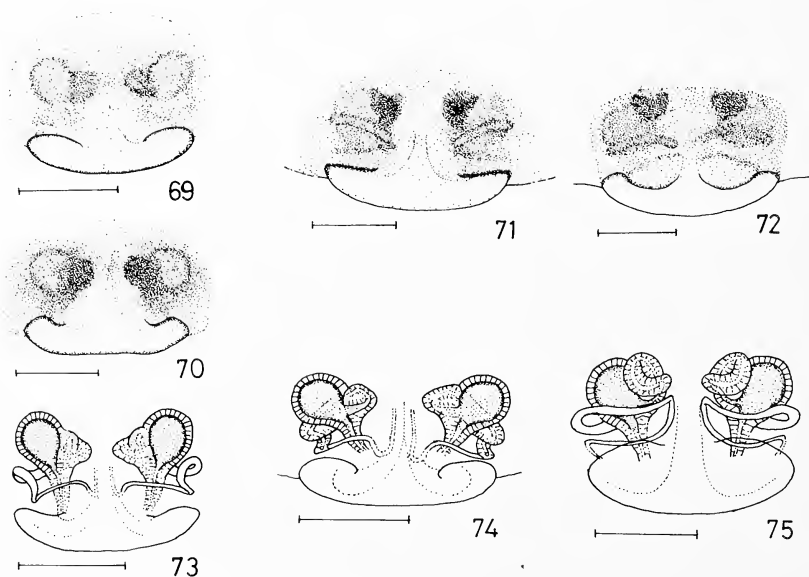
Spirembolus humilis, new species
Figures 62,64,67,70,74,84; Map 2

Spirembolus perjucundus: Chamberlin and Ivie 1945: 221; not *S. perjucundus* Crosby

Holotype.—Male holotype from Mirror Lake, Uintah Mts., Utah, July 28, 1936 (W. Ivie); deposited in AMNH.

Description.—Total length: female 1.65-1.75 mm, male 1.55 mm. Carapace: length: female 0.80 mm, male 0.70-0.75 mm. Brown to deep-brown, with dusky markings and margins. Male carapace moderately raised (Fig. 67), with usually a tiny hump in the ocular area. Abdomen: grey to black. Sternum: deep brown, suffused with black. Legs: brown. Tibial spines: female 2221, male 0011 or 0021. Tml: female 0.42-0.48, male 0.41-0.45. Male palp: Figs. 62, 64; the palpal organ is barely distinguishable from that of *S. perjucundus*. The femur and patella are long. Female palp: tibia with 3 trichobothria. Epigynum: Fig. 70; this is rather obscure in color and not very distinctive. Internal genitalia: Fig. 74.

Diagnosis.—*S. humilis* is very close to *S. perjucundus*, of which it should possibly be regarded as a sub-species. In the male, the principal difference from *S. perjucundus* lies in the lower anterior elevation of the carapace (Fig. 67 cf. Fig. 66). The females of *S. humilis* and *S. perjucundus* are barely if at all distinguishable (see also *S. perjucundus* diagnosis).



Figs. 69-75.—69, *S. perjucundus*, epigynum; 70, *S. humilis*, epigynum; 71, *S. mendax*, epigynum; 72, *S. mendax*, epigynum, another specimen; 73, *S. perjucundus*, internal genitalia, ventral; 74, *S. humilis*, internal genitalia, ventral; 75, *S. mendax*, internal genitalia, ventral (Scale lines 0.1 mm).

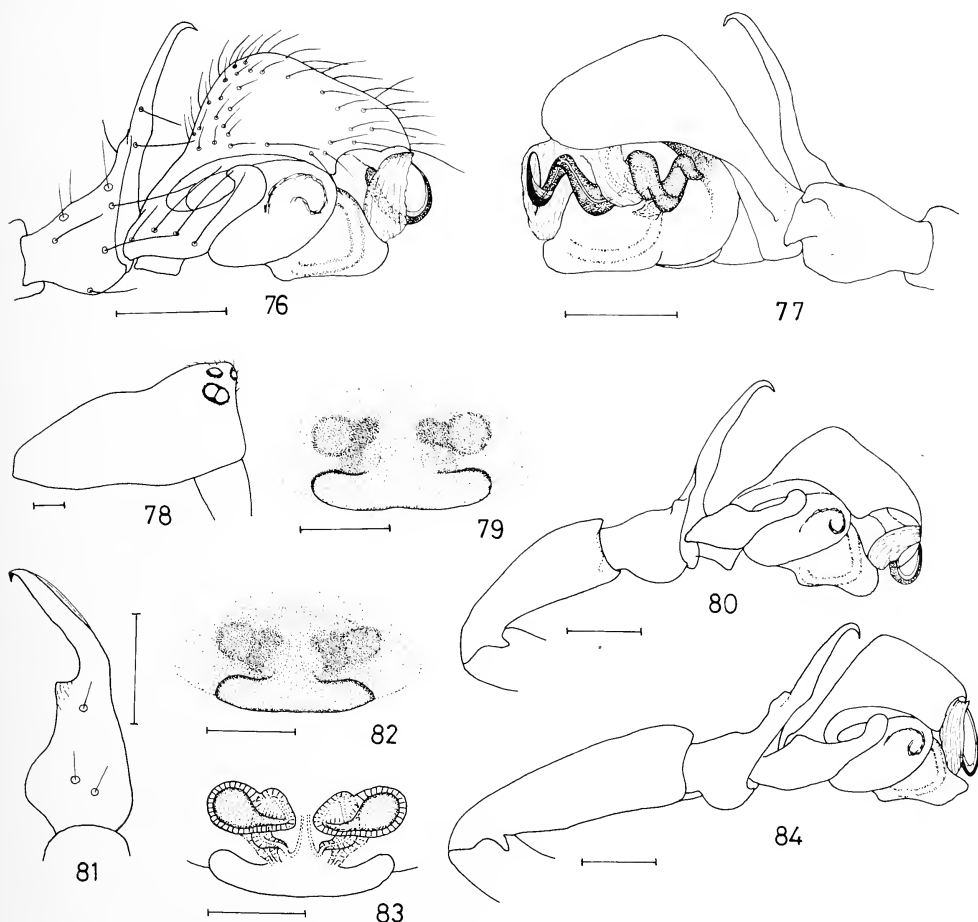
Distribution.—Known only from Utah, Oregon and northern California (Map 2).

Natural History.—Males have been taken in July and September, females in April, July and September; the main period of maturity is probably in summer. The only habitat recorded is in lombardy poplar debris in Tooele Co., Utah, at 1300 m altitude in May.

Spirembolus mendax, new species
Figures 63, 65, 68, 71, 72, 75; Map 2

Holotype.—Male holotype from Alum Rock Park, near San Jose, California, December 15, 1953 (D. Burdick); deposited in AMNH.

Description.—Total length: female 1.9-2.1 mm, male 1.7-1.8 mm. Carapace: length: female 0.90-0.95 mm, male 0.85 mm. Orange-brown to deep brown with dusky margins. Male carapace sharply and steeply elevated (Fig. 68). Abdomen: grey to black. Sternum: orange-brown, suffused with black. Legs: brown. Tibial spines: female 2221, male 0121.



Figs. 76-84.—76, *S. hibernus*, male palp, ectal; 77, *S. hibernus*, male palp, mesal; 78, *S. hibernus*, male carapace, lateral; 79, *S. hibernus*, epigynum; 80, *S. hibernus*, male palp, ectal; 81, *S. hibernus*, male palpal tibia, dorsal; 82, *S. hibernus*, epigynum, another specimen; 83, *S. hibernus*, internal genitalia, ventral; 84, *S. humilis*, male palp, ectal (Scale lines 0.1 mm).

Tml: female 0.41-0.46, male 0.37-0.40. Male palp: Figs. 63, 65; the embolus forms a coil of moderately large diameter. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 71, 72, 75.

Diagnosis.—*S. mendax* falls into Sections 7 of the Keys. The male is separated from the others in this section, and grouped with *S. perjucundus*, by the steeply raised carapace; *S. mendax* is then readily distinguished by the larger size of the embolic coil (Fig. 65 cf. Fig. 59). In the AMNH Collection, *S. mendax* male was in several instances mistaken for *S. perjucundus*. Diagnosis of the female is based on the genitalia. The epigynum can be rather similar to that of *S. phylax* (q.v.), but usually the anterior crescent-shaped markings are less clear and the more robust internal ducts show moderately clearly through the integument in *S. mendax* (Figs. 71, 72 cf. Fig. 56). *S. mendax* has stouter sperm ducts than in *S. phylax* (Fig. 75 cf. Fig. 58); the duct configuration bears a similar relationship to that of *S. perjucundus* as shown by the species pair *S. monticolens*/*S. pachygnathus*. *S. mendax* can usually be separated fairly readily from *S. falcatus* by the epigynum (Figs. 71, 72 cf. Fig. 88), coupled with the somewhat more slender legs of *S. mendax*, which has the same 1/d ratios as in *S. phylax* (q.v.).

Distribution.—Most of the records are from California, with one from Oregon (Map 2).

Natural History.—Males have been taken in December, January, February, March and May, females in December, February, April, May, June, July and September. The main period of maturity seems probably to be in the winter months. Nothing is recorded on habitat.

Spirembolus hibernus, new species
Figures 76,77,78,79,80,81,82,83; Map 2

Holotype.—Male holotype from Cleveland National Forest, 5 miles west of Henshaw Lake, California, February 16, 1958 (I. Newell); deposited in AMNH.

Description.—Total length: female 2.0-2.1 mm, male 1.6 mm. Carapace: length: female 0.80-0.85 mm, male 0.75 mm. Orange-brown with faint dusky markings. Male carapace only moderately raised (Fig. 78). Abdomen: grey to black. Sternum: yellow-brown with dusky margins. Legs: orange brown. Tibial spines: female 2221, male 0021. Tml: female 0.37-0.40, male 0.35. Male palp: Figs. 76, 77, 80, 81; the embolus forms a small coil. The patella is shorter than in *S. humilis* (Fig. 80 cf. Fig. 84). Female palp: tibia with 3 trichobothria. Epigynum: Figs. 79, 82, 83.

Diagnosis.—This species falls into Sections 7 of the Keys. In the male sex, *S. hibernus* has the palpal tibia of the same general form as in *S. perjucundus*, *S. humilis* and *S. mendax*. From *S. perjucundus* it is at once separated by the lower elevation of the carapace (Fig. 78 cf. Fig. 66), and from *S. mendax* by the much smaller diameter of the embolic coil (Fig. 77 cf. Fig. 65). From *S. humilis* the male is distinguished by the relatively shorter palpal patella and by a small difference in the SA (Fig. 80 cf. Fig. 84). In the female sex, the epigynum is similar to those of *S. perjucundus* and *S. humilis*, but normally seems to be distinguishable (Figs. 79, 82, cf. Figs. 69, 70); the internal genitalia also show small differences (Fig. 83 cf. Figs. 73, 74). *S. hibernus* female also has rather more slender legs than those of *S. perjucundus* and *S. humilis*: for *S. hibernus* tibia I 1/d is 5.5, metatarsus I 1/d is 7.5-8, cf. corresponding figures of 4.5 and 6-6.5 for *S. perjucundus* and *S. humilis*.

Distribution.—The species is recorded from a number of localities in California (Map 2).

Natural History.—Males have been taken in February, April and October, females in February, March, April, July, August and October; it seems probable that the main period of maturity is during the winter months. There is no information on habitat.

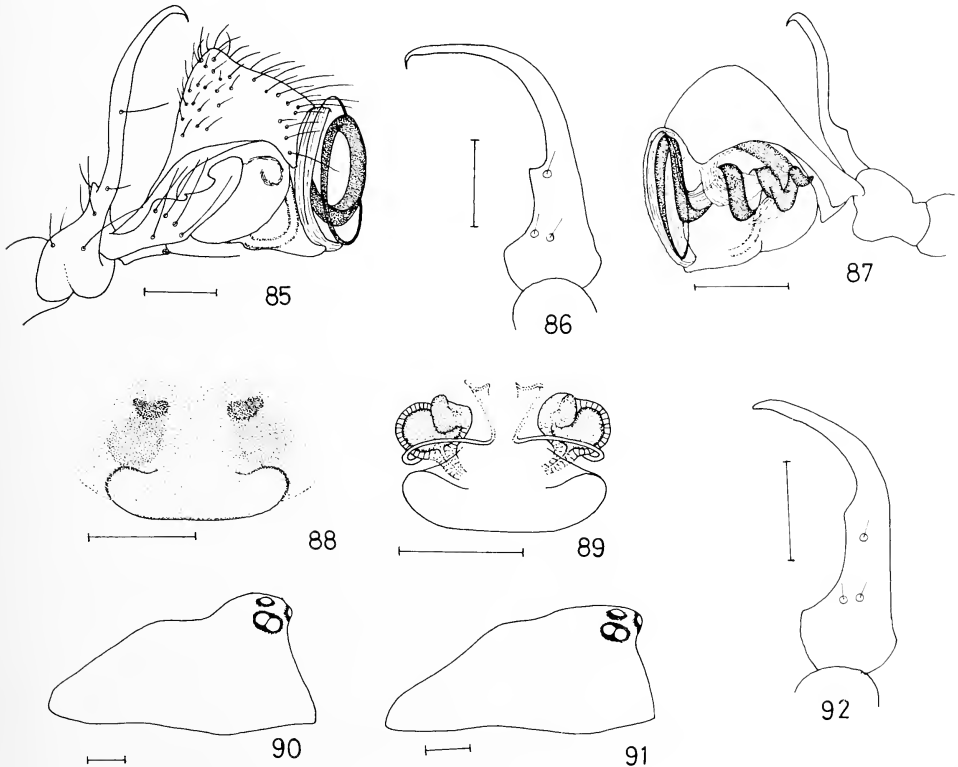
Spirembolus falcatus, new species

Figures 85,86,88,89,90; Map 2

Holotype.—Male holotype from San Jacinto Mts., California, October 29, 1955 (I. Newell); deposited in AMNH.

Description.—Total length: female 1.65-1.70 mm, male 1.60-1.65 mm. Carapace: length: female and male 0.70-0.75 mm. Yellow-brown to chestnut brown, with dusky markings and margins. Male carapace fairly sharply elevated (Fig. 90). Abdomen: grey to black. Sternum: yellow to brown, suffused with black. Legs: pale brown to brown. Tibial spines: female 2221, male 0011. Tml: female 0.46-0.55, male 0.50-0.55. Male palp: Figs. 85, 86. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 88, 89.

Diagnosis.—This species falls into Sections 7 of the Keys. The male is diagnosed by the palpal tibia, which is of the same general form as that of *S. spirotubus* and related species, but with different proportions; in addition, the white excrescence present between femur and patella in *S. spirotubus*, etc. is absent in *S. falcatus*. The male of *S. falcatus* is very



Figs. 85-92.—85, *S. falcatus*, male palp, ectal; 86, *S. falcatus*, male palpal tibia, dorsal; 87, *S. tiogensis*, male palp, mesal; 88, *S. falcatus*, epigynum; 89, *S. falcatus*, internal genitalia, ventral; 90, *S. falcatus*, male carapace, lateral; 91, *S. tiogensis*, male carapace, lateral; 92, *S. tiogensis*, male palpal tibia, dorsal (Scale lines 0.1 mm).

similar to *S. tiogensis* and *S. montivagus*, but these species show small differences in the palpal tibiae; in addition, the carapace forms distinguish *S. falcatus* and *S. tiogensis*, while *S. montivagus* is distinguished by the presence of the white excrescence between palpal femur and patella. The female of *S. falcatus* is diagnosed by the epigynum, which is rather similar to that of *S. phylax* though normally distinguishable (Fig. 88 cf. Fig. 56); the internal genitalia are probably too similar to be of value in diagnosis. The female of *S. falcatus* is most frequently smaller than *S. phylax*, and the legs are slightly stouter (see *S. phylax* diagnosis).

Distribution.—Known only from a few localities in California (Map 2).

Natural History.—Males have been taken in October, December and January, females in October and December; hence the chief period of maturity is probably in winter. There is no information on habitat.

Spirembolus tiogensis, new species

Figures 87, 91, 92; Map 2

Holotype.—Male holotype from Tioga Pass, 10,000 ft., California, September 22, 1961 (W. J. Gertsch and W. Ivie); deposited in AMNH.

Description.—Only the male is known. Total length: male 1.45 mm. Carapace: length: male 0.65 mm. Brown, with dusky markings and margins; barely raised anteriorly (Fig. 91). Abdomen: grey-black. Sternum: brown, suffused with black. Legs: brown. Tibial spines: male 0021. Tml: male 0.48. Male palp: Figs. 87, 92; the inferior apophysis on the tibia is very small.

Diagnosis.—*S. tiogensis* falls into Section 7 of the Key. It is close to *S. falcatus*, from which it is distinguished by small differences in the palpal tibia (Fig. 92 cf. Fig. 86) and in the carapace (Fig. 91 cf. Fig. 90); the embolic coil is somewhat smaller in diameter anteriorly than in *S. falcatus*. *S. tiogensis* male is also similar to *S. montivagus*: there is a small difference in the palpal tibia, and the palp of *S. montivagus* has a white excrescence between femur and patella which is lacking in *S. tiogensis*.

Distribution.—Known only from the type locality (altitude 3280 m) (Map 2).

Natural History.—Presumably this species is limited to the high mountains.

Spirembolus whitneyanus Chamberlin and Ivie

Figures 93, 94, 95, 96, 97; Map 2

Spirembolus whitneyanus Chamberlin and Ivie 1935: 20, 1945: 222; Roewer 1942: 666; Bonnet 1958: 4123

Spirembolus orthus Chamberlin 1948: 548. NEW SYNONYMY. Chamberlin does not appear to have designated a type of *S. orthus*, but there is one vial in the AMNH material which has the locality label and other data agreeing completely with the data given by Chamberlin: this contains a single female which is *S. whitneyanus*.

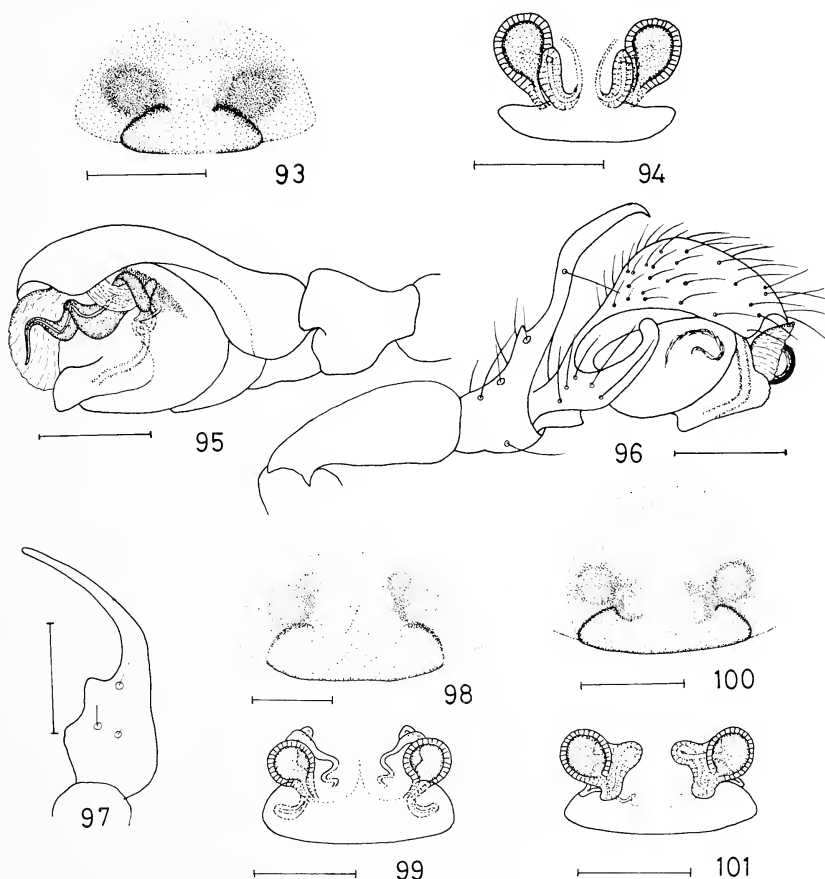
Holotype.—Male holotype, Mt. Whitney, California, August 8, 1931 (W. Ivie); in AMNH, examined.

Description.—Total length: female 1.40-1.60 mm, male 1.30-1.40 mm. Carapace: length: female: 0.70 mm, male 0.65 mm. Brown, with dusky markings and margins. Male carapace only slightly raised. Abdomen: grey. Sternum: brown, with dusky margins.

Legs: brown. Tibial spines: female 2221, male 0021 or 1121. TmI: female 0.42-0.46, male 0.40-0.44. The short curved hairs on the male tibiae and metatarsi I and II are more weakly developed than in the other members of the *spirotubus* species group. Male palp: Figs. 95, 96, 97; embolus short and rather stout, in a coil of small diameter. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 93, 94.

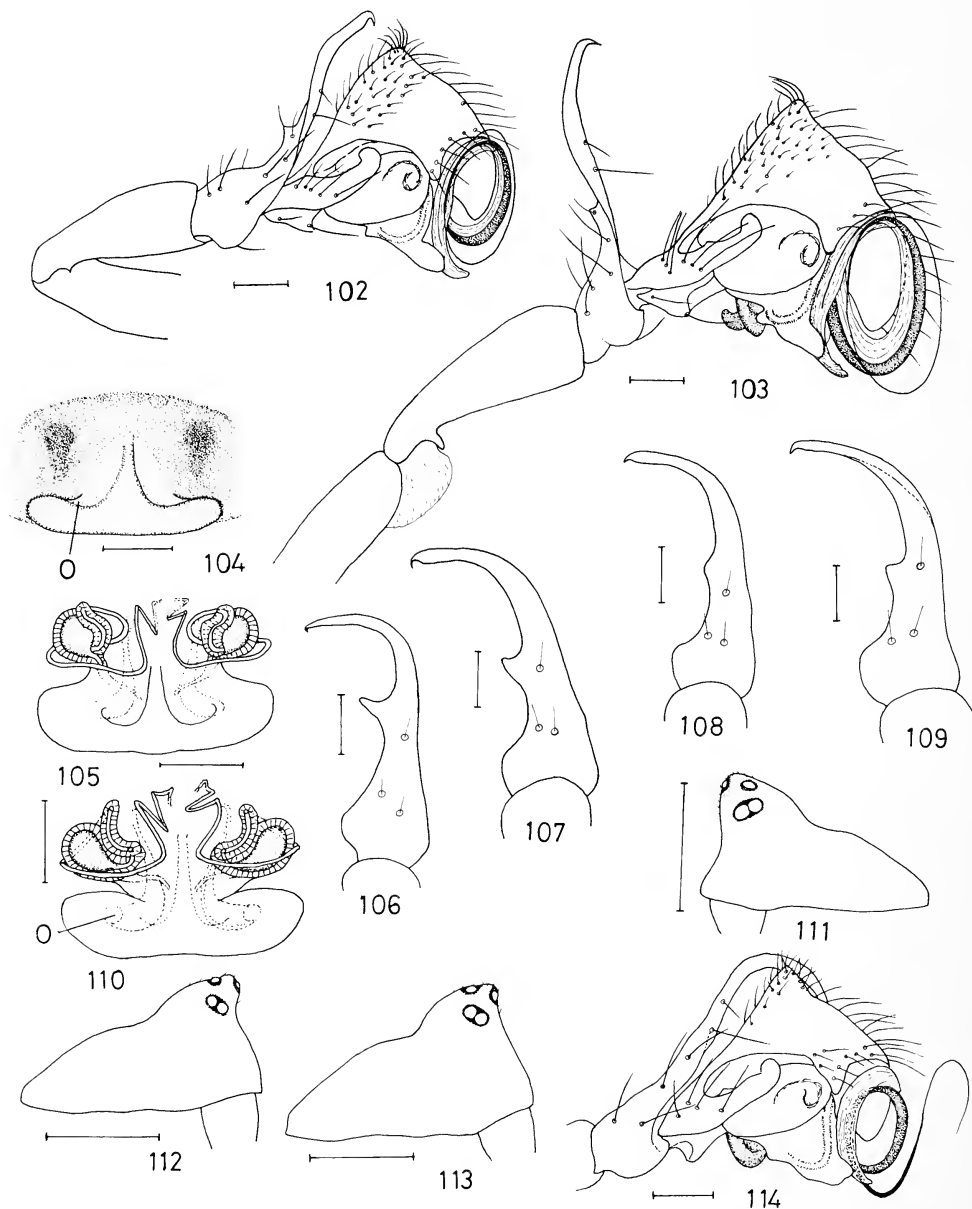
Diagnosis.—In the male, the relatively small size, the short stout embolus (Fig. 95) and the small elevation of the carapace suffice to distinguish *S. whitneyanus* from all other species falling in Section 7 of the Key. In the female, the epigynum differs sufficiently from those species grouped in Section 7 of the Key to make diagnosis fairly easy. The species most likely to be confused with *S. whitneyanus* female is *S. redondo*, but the differences are usually distinct enough (Fig. 93 cf. Fig. 186). In addition, *S. whitneyanus* female has somewhat stouter legs (e.g. tibia I 1/d is 4.4-5) than *S. redondo* (tibia I 1/D ca. 6).

Distribution.—This species has been taken on very few occasions, from a few localities in California (Map 2).



Figs. 93-101.—93, *S. whitneyanus*, epigynum; 94, *S. whitneyanus*, internal genitalia, ventral; 95, *S. whitneyanus*, male palp, meso-ventral; 96, *S. whitneyanus*, male palp, ectal; 97, *S. whitneyanus*, male palpal tibia, dorsal; 98, *S. venustus*, epigynum; 99, *S. venustus*, epigynum, cleared; 100, *S. chilkatensis*, epigynum; 101, *S. chilkatensis*, internal genitalia, ventral (Scale lines 0.1 mm).

Natural History.—Adults of both sexes have been taken in August and September; the chief period of maturity may therefore be in summer. The only habitat mentioned is under stones near water, at Mono Lake, California.



Figs. 102-114.—102, *S. mundus*, male palp, ectal; 103, *S. latebricola*, male palp, ectal; 104, *S. mundus*, epigynum; 105, *S. mundus*, internal genitalia, ventral; 106, *S. elevatus*, male palpal tibia, dorsal; 107, *S. mundus*, male palpal tibia, dorsal; 108, *S. mundus*, male palpal tibia, dorsal (another specimen); 109, *S. latebricola*, male palpal tibia, dorsal; 110, *S. mundus*, internal genitalia, ventral (another specimen); 111, *S. elevatus*, male carapace, lateral; 112, *S. mundus*, male carapace, lateral; 113, *S. latebricola*, male carapace, lateral; 114, *S. elevatus*, male palp, ectal. Abbreviation: O, probable position of opening to spermathecal duct (Scale lines 0.1 mm, except Figs. 111, 112, 113, 0.5 mm).

Spirembolus venustus, new species
Figures 98, 99; Map 2

Holotype.—Female holotype from Sabino Canyon, near Tucson, Arizona, June 5, 1952 (W. J. Gertsch, M. Cazier and R. Schrammel); deposited in AMNH.

Description.—Only the female is known. Total length: female 2.0 mm. Carapace: length: female 0.90 mm. Pale orange. Abdomen: grey. Sternum: yellow. Legs: orange-brown. Tibial spines: female 2221. TmI: female 0.40. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 98, 99.

Diagnosis.—The epigynum, coupled with the rather attractive color, distinguish this species from all others falling in Section 7 of the Key.

Distribution.—Known only by the holotype (Map 2).

Natural History.—Nothing known.

Spirembolus chilkatensis (Chamberlin and Ivie), new combination
Figures 100, 101; Map 4

“*Erigone*” *chilkatensis* Chamberlin and Ivie 1947: 38

Holotype.—Female holotype from Haines, Alaska, August 20-25, 1945 (J. C. Chamberlin); in AMNH, examined.

Description.—Only the female is known. Total length: female 1.9-2.3 mm. Carapace: length: female 0.8-1.0 mm. Orange-brown, with dusky markings and margins. Abdomen: grey. Epigastric plates with closely spaced striae. Sternum: yellow, with dusky margins. Legs: brown. Tibial spines: female 2221. TmI: female 0.50-0.55. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 100, 101.

Diagnosis.—This species falls in Section 7 of the Key. The presence of striae on the epigastric plates, coupled with the form of the epigynum are sufficient to distinguish this species from all others in Section 7.

Distribution.—This species is known from two localities near the north-west coast: Alaska (the type) and Oregon (two paratype females) (Map 4).

Natural History.—The females were taken in August and November. Nothing is known on habitat.

Spirembolus mundus Chamberlin and Ivie
Figures 102, 104, 105, 107, 108, 110, 112; Map 2

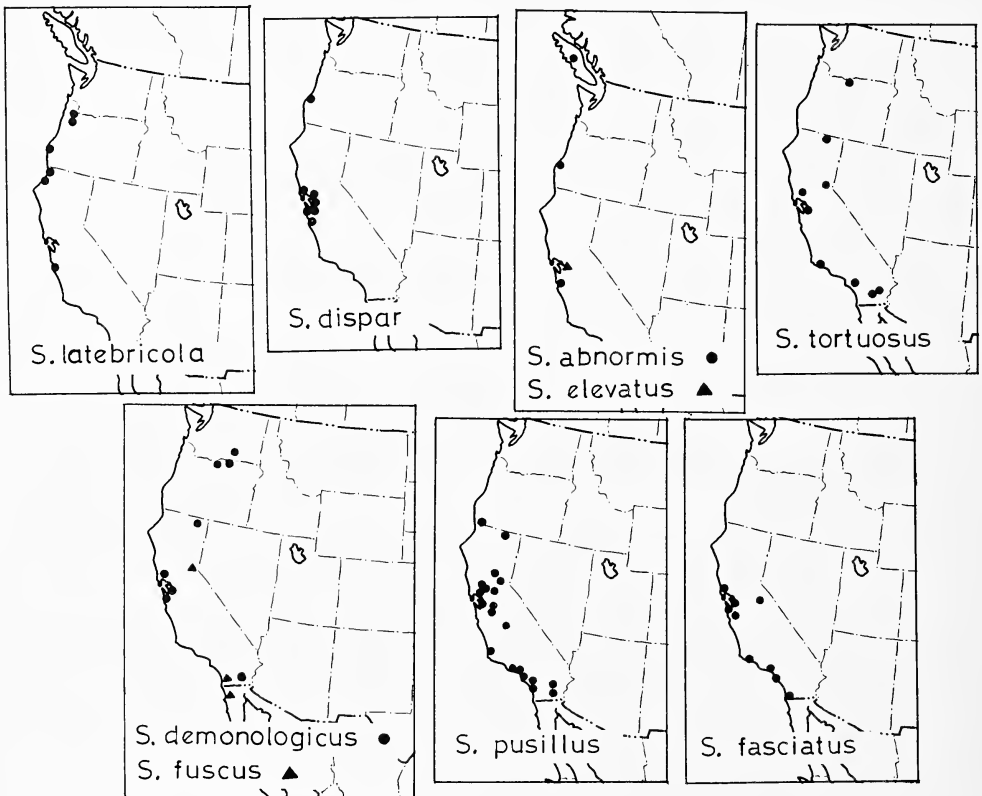
Spirembolus mundus Chamberlin and Ivie 1933: 18, 1945: 218; Roewer 1942: 666; Bonnet 1958: 4122.

Holotype.—Male holotype from Clear Creek, Raft River Mts., Utah, September 4, 1932 (R. V. Chamberlin and W. Ivie); in AMNH, examined.

Description.—Total length: female 2.8-3.0 mm, male 2.40-2.60 mm. Carapace: length: female 1.15-1.30 mm, male 1.05-1.10 mm. Reddish brown or orange, with dusky markings and margins. Male carapace moderately steeply raised (Fig. 112). Abdomen: shiny black. Sternum: brown, suffused with black particularly on margins. Legs: orange-brown to yellow-brown. Tibial spines: female 2221, male 0021. TmI: female and male

0.60-0.68. Male palp: Figs. 102, 107, 108; the cymbium is raised almost to a point, and the embolus forms a fairly wide coil. There is a small white excrescence between femur and patella. The size of the inferior apophysis on the tibia is somewhat variable. Female palp: tibia with 3 trichobothria. Epigynum: Fig. 104. Internal genitalia: Figs. 105, 110; the appearance is somewhat variable depending on the angle taken up by the spermathecae.

Diagnosis.—The high value of TmI places this species in Section 5 of the Keys. The males of *S. mundus* and *S. latebricola* are separated easily from *S. elevatus*, *S. dispar* and *S. abnormis* by a combination of the larger size, the brighter color of the carapace and legs, the form of the carapace (Figs. 112, 113 cf. Figs. 111, 118, 124) and the form of the palpal tibia (Figs. 107, 109 cf. Figs. 106, 122, 125). *S. mundus* male is distinguished from *S. latebricola* by the somewhat smaller diameter of the embolic coil and the slightly shorter palpal patella (Fig. 102 cf. Fig. 103). The female of *S. mundus* is separated from *S. dispar* and *S. abnormis* by the size, color and the epigynum (Fig. 104 cf. Figs. 117, 120). Females of *S. mundus* and *S. latebricola* seem not to be distinguishable. In the Museum material, there were several instances where the female of *Coreorgonal monoceros* (Simon) had been mistaken for *S. mundus*; although the females of these two species are very similar in general appearance, e.g. in size, color and value of TmI, the epigyna are in fact readily distinguishable. The genus *Coreorgonal* will be dealt with in a following paper.



Map 3.—Western North America: distributions of *S. latebricola*, *S. dispar*, *S. abnormis*, *S. elevatus*, *S. tortuosus*, *S. demonologicus*, *S. fuscus*, *S. pusillus* and *S. fasciatus*.

Distribution.—The species has been recorded from Utah, Idaho, Oregon, Washington and British Columbia (Map 2).

Natural History.—Males and females have been taken in all months except February, July and August. The habitats recorded are: amongst dead leaves (in April and September, Utah), on grapes (in September, Oregon), inside a house (in November, Oregon) and aeronauting (in November, Oregon).

Spirembolus latebricola, new species

Figures 103, 109, 113; Map 3

Holotype.—Male holotype from Patrick Point State Park, California, September 21, 1964 (J. and W. Ivie); deposited in AMNH.

Description.—Total length: female 2.6-3.1 mm, male 2.7-2.9 mm. Carapace: length: female 1.10-1.30 mm, male 1.10-1.20 mm. Brown to orange-brown, with dusky markings and margins. Although there is always some variation, the male carapace (Fig. 113) is normally somewhat more steeply raised than that of *S. mundus*. Abdomen: shiny black. Sternum: orange-brown, suffused with black. Legs: orange-brown. Tibial spines: female 2221, male 0021. Tml: female 0.62-0.65, male 0.60-0.62. Male palp: Figs. 103, 109; very similar to *S. mundus*, but the embolic coil is larger in diameter. There is a white excrescence, sometimes quite large, between femur and patella. Female palp: tibia with 3 trichobothria. Female genitalia: not distinguishable from those of *S. mundus*.

Diagnosis.—This is dealt with under the diagnosis of *S. mundus*.

Distribution.—This species is known from a few localities in California and Oregon (Map 3).

Natural History.—Both sexes were taken in September and October; nothing was recorded on habitat.

Spirembolus elevatus, new species

Figures 106, 111, 114; Map 3

Holotype.—Male holotype from Berkeley, California, November 1919 (H. Dietrich); deposited in AMNH. This specimen was labelled by Crosby "*Spirembolus perjucundus*. Paratype".

Description.—Only the male is known. Total length: male 1.65 mm. Carapace: length: male 0.85 mm. Steeply raised anteriorly (Fig. 111). Abdomen: grey-black. Sternum: yellow, suffused with grey. Legs: pale yellow. Tibial spines: male 0021. Tml: male 0.67. Male palp: Figs. 106, 114; the cymbium is raised almost to a point, as in *S. mundus*. There is a small excrescence between femur and patella. The specimen is practically 60 years old, and it is probable that new specimens will be more deeply colored.

Diagnosis.—The high value of Tml places this species in Section 5 of the Key with *S. mundus*, *S. latebricola*, *S. dispar* and *S. abnormis*. *S. elevatus* is distinguished from these four species by a combination of the form of the carapace (Fig. 111) and of the palpal tibia (Fig. 106). The palpal tibia is of the same general pattern as those of *S. mundus* and *S. latebricola*, but size alone will prevent any confusion with these two species.

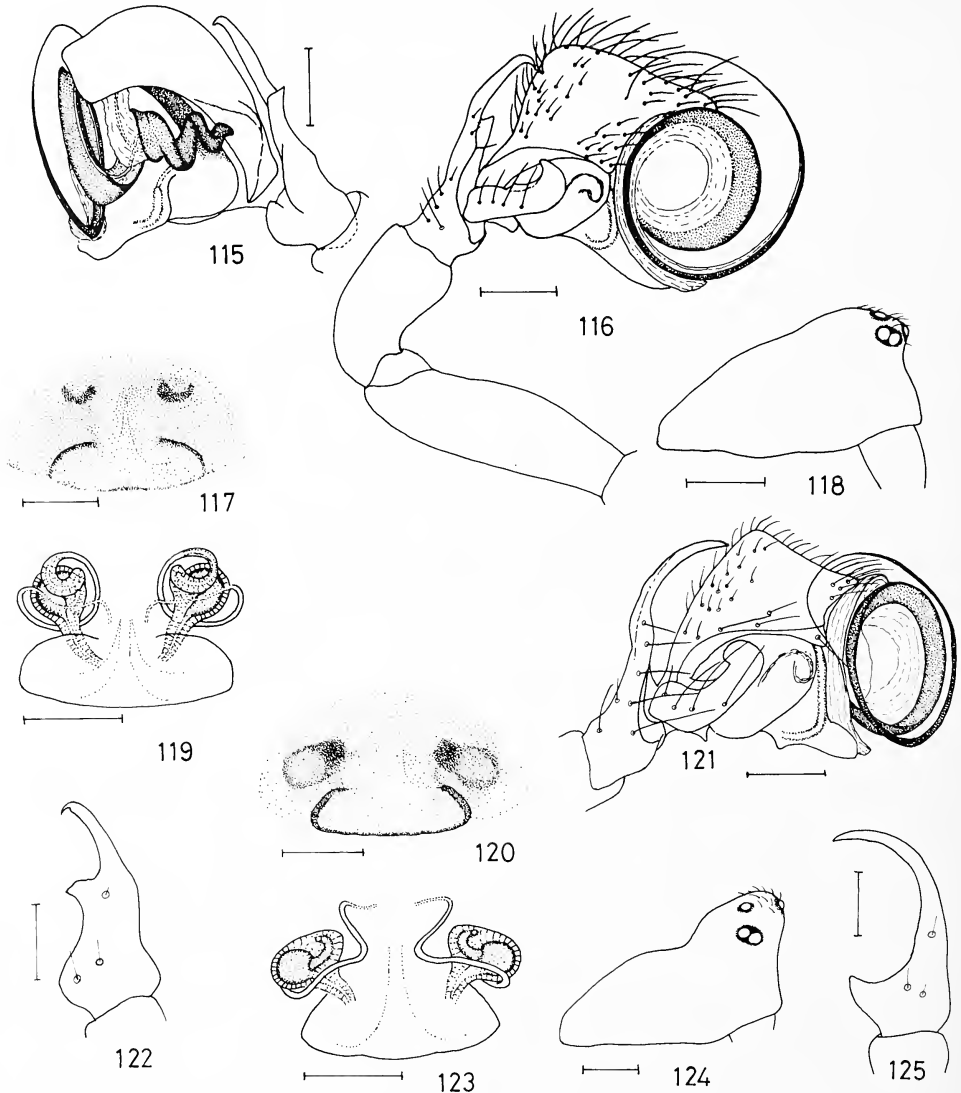
Distribution.—Known only from the holotype (Map 3).

Natural History.—There is no information on habitat.

Spirembolus dispar, new species
Figures 115, 116, 117, 118, 119, 122; Map 3

Holotype.—Male holotype from Pebble Beach, California, March 25, 1957 (A. M. Nadler); deposited in AMNH.

Description.—Total length: female 1.9-2.1 mm, male 1.7 mm. Carapace: length: female 0.80-0.85 mm, male 0.75-0.80 mm. Brown, with dusky markings and margins. Male carapace not greatly raised (Fig. 118). Abdomen: black. Sternum: brown, suffused with



Figs. 115-125.—115, *S. dispar*, male palp, mesal; 116, *S. dispar*, male palp, ectal; 117, *S. dispar*, epigynum; 118, *S. dispar*, male carapace, lateral; 119, *S. dispar*, internal genitalia, ventral; 120, *S. abnormis*, epigynum; 121, *S. abnormis*, male palp, ectal; 122, *S. dispar*, male palpal tibia, dorsal; 123, *S. abnormis*, internal genitalia, ventral; 124, *S. abnormis*, male carapace, lateral; 125, *S. abnormis*, male palpal tibia, dorsal (Scale lines 0.1 mm, except Figs. 118, 124, 0.2 mm).

black. Legs: brown to pale brown. Tibial spines: female 2221, male 0021. Tml: female and male 0.75-0.80. Male palp: Figs. 115, 116, 122; the embolus forms a wide coil anteriorly. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 117, 119.

Diagnosis.—The high value of Tml places this species in Section 5 of the Keys. The male of *S. dispar* is separated clearly from the other members of this group by a combination of the form of the palpal tibia (Fig. 122 cf. Figs. 106, 107, 109, 125) and of the carapace (Fig. 118 cf. Figs. 111, 112, 113, 124). The female is readily distinguished from the others in the group by the epigynum (Fig. 117 cf. Figs. 104, 120). *S. dispar* is smaller and less striking in color than *S. mundus* and *S. latebricola*, and has a higher value of Tml.

Distribution.—Recorded from California and Oregon only (Map 3).

Natural History.—Both sexes were taken in January, March, April and September; most specimens were taken in January/March. Nothing is known on habitat.

Spirembolus abnormis, new species
Figures 120, 121, 123, 124, 125; Map 3

Holotype.—Male holotype from Wellington, Vancouver Island, British Columbia. October 1-15, 1951 (R. Guppy); deposited in AMNH.

Description.—Total length: female 1.9-2.1 mm, male 2.0 mm. Carapace: length: female and male 0.90-0.95 mm. Brown, with faint dusky markings and margins. Male carapace steeply raised (Fig. 124). Abdomen: grey to black. Sternum: brown, heavily suffused with black. Legs: orange-brown. Tibial spines: female 2221, male 0021. Tml: female 0.75-0.80, male 0.70-0.75. Male palp: Figs. 121, 125; the embolus forms a wide coil anteriorly. Female palp: tibia with 3 trichobothria. Epigynum: Figs. 120, 123.

Diagnosis.—The high value of Tml places this species in Section 5 of the Keys. The male of *S. abnormis* is separated clearly from the other species in the Section by the combination of the steeply raised carapace (Fig. 124) and the form of the palpal tibia (Fig. 125 cf. Figs. 106, 107, 109, 122). The female is readily distinguished from the other species by the epigynum (Fig. 120 cf. Figs. 104, 117). *S. abnormis* is smaller and less striking in color than *S. mundus* and *S. latebricola*.

Distribution.—The few records are from the western coastal area: California, Oregon and British Columbia (Map 3).

Natural History.—Males have been taken in April, September and October. females in July and October. Nothing is known on habitat.

Spirembolus tortuosus (Crosby in Chamberlin 1925), new combination
Figures 126, 127, 128, 129, 130, 131; Map 3

Tortembolus tortuosus Crosby in Chamberlin 1925: 116, Roewer 1942: 667; Bonnet 1958: 4663.

Holotype.—Male holotype from Stanford, California, 1920-1921; in MCZ, examined.

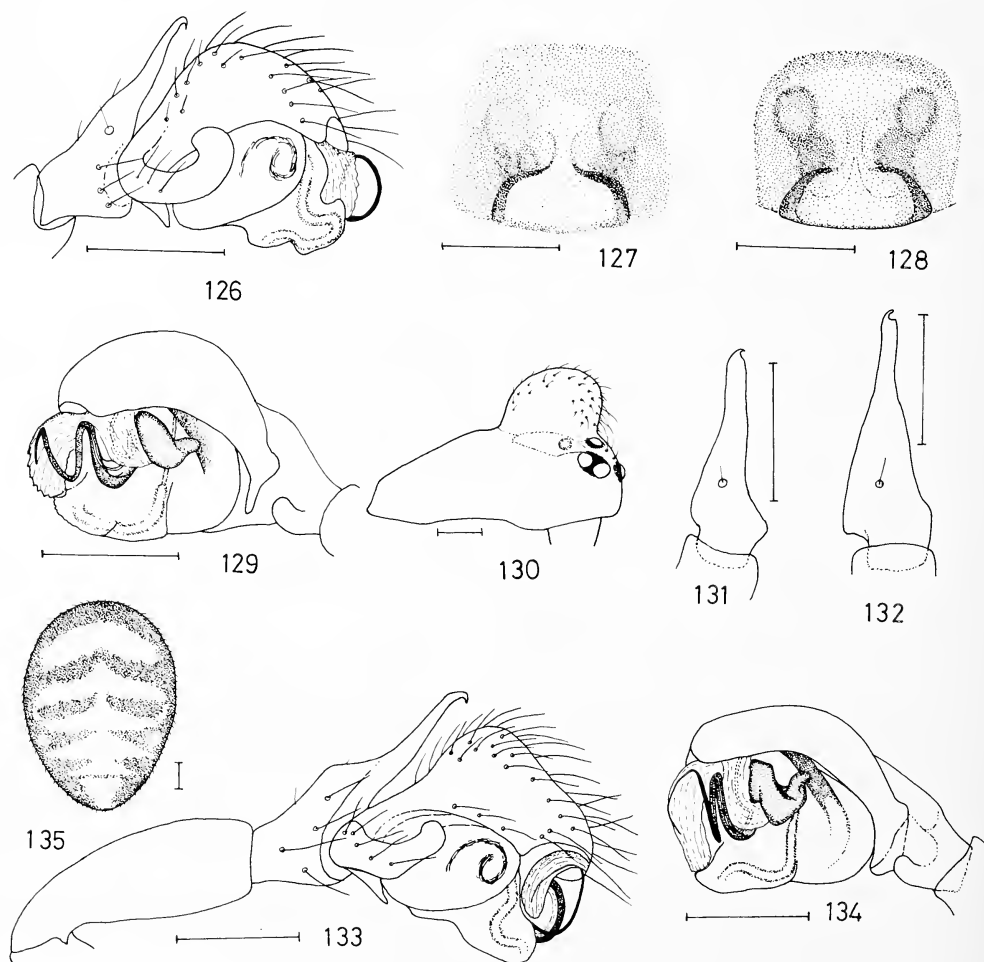
Description.—The female, which has been taken with the male, is described for the first time. Total length: female 1.30-1.40 mm, male 1.15-1.25 mm. Carapace: length: female 0.60-0.65 mm, male 0.55 mm. Brown to deep brown, with darker margins. Male carapace raised into large lobe with holes and sulci on sides (Fig. 130). Abdomen: grey to black. Epigastric plates smooth, without striae. Sternum: brown, suffused with black.

Legs: brown. Tibial spines: female 2221, male 0011. TmI: female 0.46-0.48, male 0.42-0.44. Male palp: Figs. 126, 129, 131; the embolus forms a small coil, and the tailpiece is rather compressed. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 127, 128. The internal genitalia are close to those of *S. demonologicus*.

Diagnosis.—In the male, the large lobe on the carapace, coupled with the unicolorous abdomen and the absence of striae on the epigastric plates, distinguish *S. tortuosus* from all other species. The female falls into Section 6 of the Key; from the other species in this Section *S. tortuosus* is readily separated by the epigynum (Figs. 127, 128) and its relatively small size offers confirmation of identity.

Distribution.—Most of the records are from California, with one from Oregon (Map 3).

Natural History.—Males have been taken in October, November and January, females in September, October, December, January and February/March; the main period of maturity seems therefore to be in winter. Nothing is recorded on habitat.



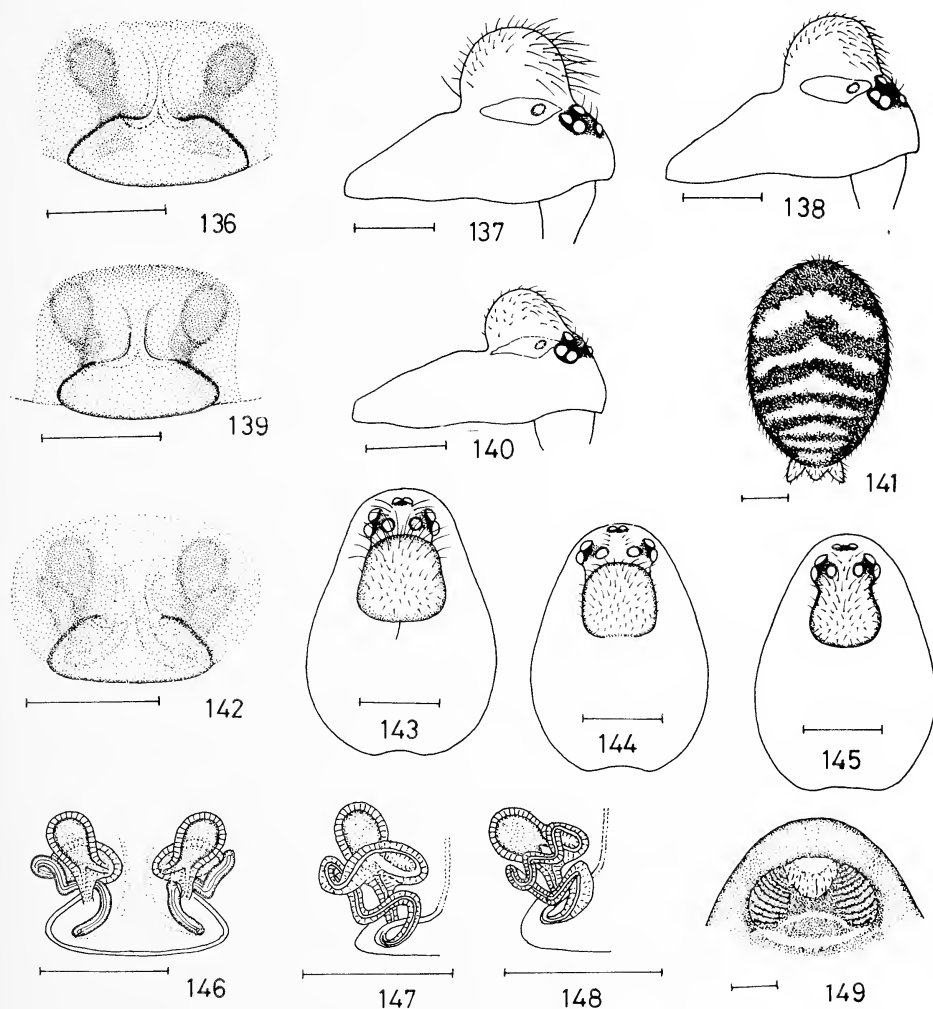
Figs. 126-135.—126, *S. tortuosus*, male palp, ectal; 127, *S. tortuosus*, epigynum; 128, *S. tortuosus*, epigynum (another specimen); 129, *S. tortuosus*, male palp, mesal; 130, *S. tortuosus*, male carapace, lateral; 131, *S. tortuosus*, male palpal tibia, dorsal; 132, *S. pusillus*, male palpal tibia, dorsal; 133, *S. pusillus*, male palp, ectal; 134, *S. pusillus*, male palp, mesal; 135, *S. fuscus*, abdomen, dorsal (Scale lines 0.1 mm).

Spirembolus fuscus, new species

Figure 135; Map 3

Holotype.—Female holotype from 4 miles west of Newcastle, California, April 1958 (I. M. Smith and R. Schuster); deposited in AMNH.

Description.—Only the female is known. Total length: female 1.25-1.30 mm. Carapace: length: female 0.60-0.65 mm. Deep brown with dusky margins. Abdomen: black, with bold white chevrons dorsally (Fig. 135); ventrally black, with any white markings not extending into central zone. Epigastric plates smooth. Sternum: deep brown, suffused with black. Legs: orange-brown. Tibial spines: very short and weak, and



Figs. 136-149.—136, *S. demonologicus*, epigynum; 137, 138, 140, *S. demonologicus*, forms of male carapace, lateral; 139, *S. demonologicus*, epigynum (another specimen); 141, *S. pusillus*, abdomen, dorsal; 142, *S. pusillus*, epigynum (one form); 143, 144, 145, *S. demonologicus*, forms of male carapace, dorsal; 146, *S. pusillus*, internal genitalia, ventral; 147, *S. pusillus*, half of internal genitalia, dorsal; 148, *S. levis*, half of internal genitalia, dorsal; 149, *S. pusillus*, epigastric plates, male (Scale lines 0.1 mm, except Figs. 137, 138, 140, 141, 143, 144, 145, 0.2 mm).

mostly missing from the available specimens. TmI: female 0.40-0.45. Female palp: tibia with 2 trichobothria. Epigynum: identical with that of *S. tortuosus*.

S. fuscus is very close to *S. tortuosus*, the only discernible difference being in the patterned abdomen. It is to be expected that the male of *S. fuscus* will have the cephalic lobe and palps virtually identical with those of *S. tortuosus*.

Diagnosis.—The patterned abdomen and the smooth epigastric plates place this species (female) with *S. fasciatus*, *S. levis* and *S. erratus*. The epigynum separates it at once from *S. fasciatus* and *S. erratus* (Fig. 127 cf. Figs. 155, 164). *S. fuscus* and *S. levis* have very similar epigyna, which are distinguishable when viewed side by side, but which may not be completely reliable for diagnosis. The significant difference in size (*S. fuscus* being much the smaller) may be the best means for separating these two species.

Distribution.—The species is known from two localities in California (Map 3).

Natural History.—The female were taken in December, March and April. Nothing is recorded on habitat.

Spirembolus demonologicus (Crosby in Chamberlin 1925), new combination

Figures 136, 137, 138, 139, 140, 143, 144, 145; Map 3

Tortembolus demonologicus Crosby in Chamberlin 1925: 117; Roewer 1942: 667; Bonnet 1958: 4662

Holotype.—Male holotype from Berkeley, California, December 1919; in MCZ, examined.

Description.—The female, which was taken in company with the male, is described for the first time. Total length: female 1.6-1.75 mm, male 1.35-1.45 mm. Carapace: length: female and male 0.70-0.75 mm. Brown, with dusky margins. Male carapace raised into lobe, which has one of the 3 forms shown in Figs. 137, 138, 140; the holotype has the form shown in Fig. 137, which seems to be the commonest and is regarded as the "typical" form. Abdomen: grey. The epigastric plates have clear striae, fairly widely spaced in the male, somewhat more closely spaced in the female. Sternum: yellow to yellow-brown, with dusky margins. Legs: yellow-brown. Tibial spines: female 2221, male 0011. TmI: female 0.45-0.48, male 0.45. Male palp: this is identical with that of *S. pusillus* (Figs. 132, 133, 134); it is also very similar to that of *S. tortuosus*. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 136, 139; this is identical with that of some forms of *S. pusillus*, and very close to that of *S. tortuosus*. The internal genitalia appear to be identical with those of *S. pusillus*, but the ducts are always less pigmented and consequently less easy to see.

Diagnosis.—The unicolorous abdomen and the presence of strong striae on the epigastric plates group this species with *S. monicus*. The male of *S. demonologicus* is distinguished clearly from *S. monicus* by the palpal organs, the embolic coil being small in *S. demonologicus* and very large in *S. monicus* (Fig. 134 cf. Fig. 170), and by the form of the carapace (Fig. 137, 138, 140 cf. Fig. 166). In the female, the genitalia give a clear separation between *S. demonologicus* and *S. monicus* (Figs. 136, 139 cf. Fig. 171). Care should be taken not to confuse *S. demonologicus* with *S. tortuosus*; the clear difference between these two species lies in the presence or absence of distinct striae on the epigastric plates.

Distribution.—Recorded from California, Oregon and Washington (Map 3).

Natural History.—Males have been taken in September, October, November, December and January, females in September, October, November and February; the main period of maturity seems therefore to be in autumn/winter. Nothing is recorded on habitat.

Spirembolus pusillus, new species

Figures 132, 133, 134, 141, 142, 146, 147, 149; Map 3

Holotype.—Male holotype from Riverside, Riverside County, California, January 6, 1957 (I. Newell); deposited in AMNH.

Description.—Total length: female 1.40-1.60 mm, male 1.30-1.35 mm. Carapace: length: female 0.70-0.75 mm, male 0.70 mm. Orange-brown, with dusky markings and margins. Male carapace raised into 3 distinct forms (Figs. 137, 138, 140) exactly as in *S. demonologicus*; the holotype has the form shown in Fig. 137. Abdomen: black with clear white chevrons dorsally (Fig. 141); ventrally the white markings are almost absent. Both sexes with clear striae on the epigastric plates, fairly widely spaced in the male (Fig. 149), less widely spaced in the female. Sternum: brown, suffused with black. Legs: brown to orange-brown. Tibial spines: female 2221, male 0021. Tml: female 0.45-0.48, male 0.45-0.47. Male palp: Figs. 132, 133, 134. Female palp: tibia with 2 trichobothria. Epigynum: this is variable in appearance; often the ducts are clearly visible through the integument (Fig. 142), sometimes they are indistinctly visible (Fig. 136) or almost invisible. The degree of pigmentation of the sperm ducts is variable (Figs. 146, 147).

S. pusillus is very close to *S. demonologicus*, the only obvious difference being in the patterned abdomen.

Diagnosis.—The patterned abdomen and the striated epigastric plates place *S. pusillus* with *S. erratus* (some specimens), *S. novellus* and *S. praelongus*. In the male, the small embolic coil immediately separates *S. pusillus* from the three species mentioned (Fig. 134 cf. Figs. 152, 161, 170), and the identity is confirmed by the form of the carapace and of the palpal tibia (note: the carapace (Fig. 138) can be very similar to that of *S. novellus*). The female of *S. pusillus* is separated from the other three species by the genitalia (Figs. 136, 142, 146 cf. Figs. 156, 160; 164, 165; 171, 172).

Distribution.—Known from a number of localities in California and one in Oregon (Map 3).

Natural History.—Males were taken in September, October, November, December and January, being most numerous in the two latter months; females occurred in all months except May, July, August and September. The chief season of maturity seems to be in winter. The only habitat recorded is in pyracantha litter at Davis, Yolo Co. (California).

Spirembolus levis, new species

Figure 148; Map 4

Holotype.—Male holotype from south of Hemet, California, November 10, 1957 (I. Newell); deposited in AMNH.

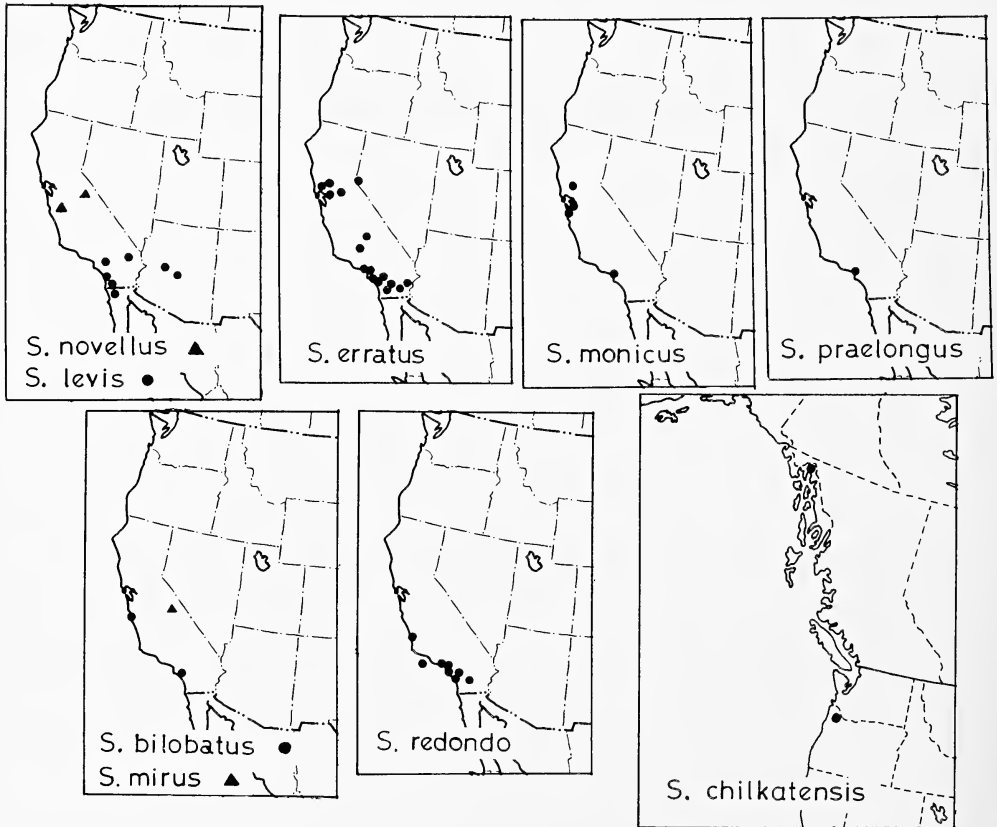
Description.—Total length: female 1.8-1.9 mm, male 1.45 mm. Carapace: length: female 0.75 mm, male 0.70 mm. Orange-brown, with dusky margins. Male with large lobe anteriorly, as in Fig. 137. Abdomen: grey-black with clear white chevrons dorsally; the white markings extend to the center of the ventral side. Epigastric plates smooth or with faint very closely spaced striae. Sternum: yellow to orange-brown, with blackish margins.

Legs: brown. Tibial spines: female 2221, male 0011. TmI: female 0.44-0.45, male 0.41-0.44. Male palp: not distinguishable from that of *S. pusillus* (Fig. 133). Female palp: tibia with 2 trichobothria. Epigynum: not distinguishable from that of *S. pusillus*. The sperm duct is more convoluted on the dorsal side of the spermatheca than in *S. pusillus* (Fig. 148 cf. Fig. 147).

Diagnosis.—The patterned abdomen and the absence of striae on the epigastric plates place *S. levis* with *S. fasciatus* in the male sex, and with *S. fasciatus*, *S. erratus* and *S. fuscus* in the female sex. In the male, the small embolic coil separates *S. levis* from *S. fasciatus* (Fig. 134 cf. Fig. 150), and the identity is confirmed by the form of the carapace and of the palpal tibia. In the female, the genitalia separate *S. levis* clearly from *S. fasciatus* and *S. erratus* (Fig. 142 cf. Figs. 155, 164). For the separation from *S. fuscus*, see that species. Care should be taken not to confuse *S. levis* with *S. pusillus*; these two species are separated solely by the presence or absence of striae on the epigastric plates.

Distribution.—This species has been found in California, Baja California and Arizona (Map 4).

Natural History.—Only two males are known, taken in March and November; females have occurred in February, March, April and November. It seems probable that the main maturity period is in winter. The only habitat recorded is in oak litter at San Bernadino Co., California.



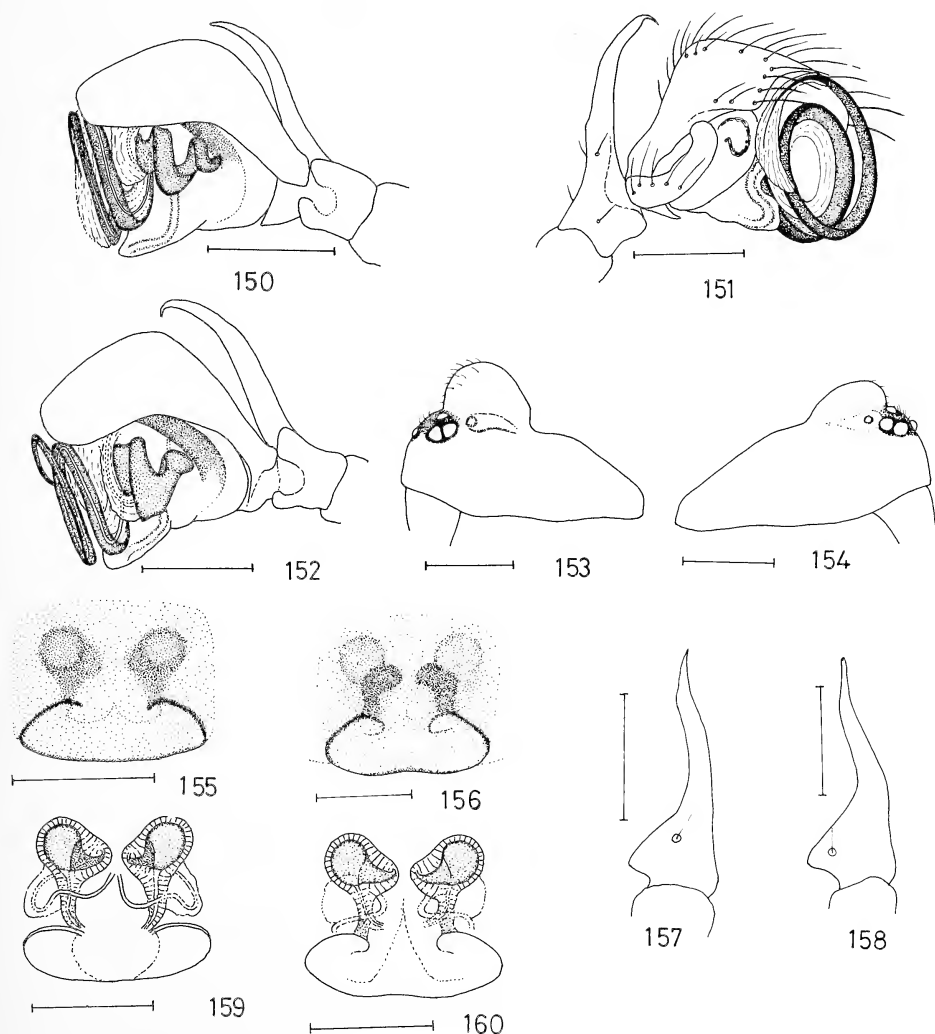
Map 4.—Western North America: distributions of *S. levis*, *S. novellus*, *S. erratus*, *S. monicus*, *S. praelongus*, *S. bilobatus*, *S. mirus*, *S. redondo* and *S. chilkatensis*.

Spirembolus fasciatus (Banks), new combination

Figures 150, 154, 155, 157, 159; Map 4

Lophocarenum fasciatum Banks 1904: 347*Tortembolus fasciatus*: Crosby 1925: 115; Roewer 1942: 667; Bonnet 1958: 4662*Diplocephalus castigatorius* Crosby 1905: 325, 1925: 115

Holotype.—Male holotype from Claremont, California (Baker); in MCZ, examined. This type is almost destroyed: only the carapace (without legs or palps) and a shrunk abdomen remain.

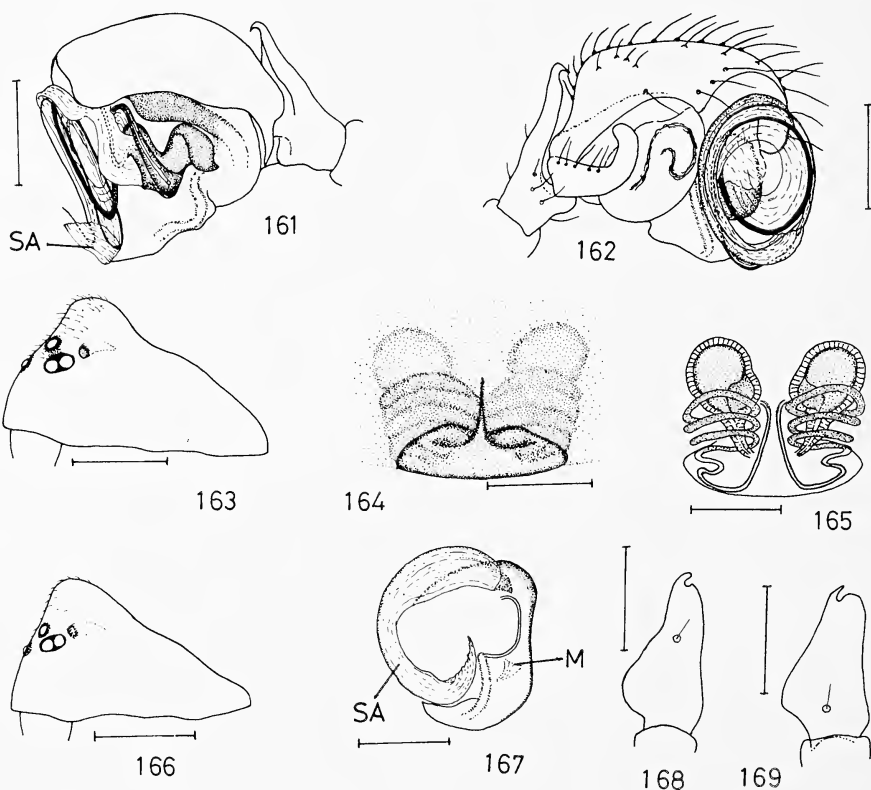


Figs. 150-160.—150, *S. fasciatus*, male palp, mesal; 151, *S. novellus*, male palp, ectal; 152, *S. novellus*, male palp, mesal; 153, *S. novellus*, male carapace, lateral; 154, *S. fasciatus*, male carapace, lateral; 155, *S. fasciatus*, epigynum; 156, *S. novellus*, epigynum; 157, *S. fasciatus*, male palpal tibia, dorsal; 158, *S. novellus*, male palpal tibia, dorsal; 159, *S. fasciatus*, internal genitalia, ventral; 160, *S. novellus*, internal genitalia, ventral (Scale lines 0.1 mm, except Figs. 153, 154, 0.2 mm).

Description.—The species here described agrees with the holotype in the form of the male head and in the virtual absence of striae on the epigastric plates, and is believed to be the true *S. fasciatus* (Banks). The types of *Diplocephalus castigatorius* (males) from AMNH were also examined, and their identity with the species described here was confirmed.

Total length: female 1.20-1.30 mm, male 1.25 mm. Carapace: length: female and male 0.55-0.60 mm. Yellow-brown. Male carapace raised into a fairly shallow lobe (Fig. 154). Abdomen: black, with white bars/chevrons dorsally, and a wide white bar ventrally just in front of the spinners. Epigastric plates normally smooth, but very faint striae are occasionally visible in the male. Sternum: yellow-brown with dusky margins. Legs: yellow-brown. Tibial spines: female 2221, male 0011 but spines weak. Tml: female 0.40, male 0.38. Male palp: Figs. 150, 157; embolic coil large. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 155, 159.

Diagnosis.—The patterned abdomen and the virtually smooth epigastric plates group the male of *S. fasciatus* with *S. levis*, from which it is readily separated by the palps (Fig. 150 cf. Fig. 134) and the form of the carapace. The female of *S. fasciatus* falls into the same grouping as *S. levis*, *S. fuscus* and *S. erratus* (those specimens which have smooth



Figs. 161-169.—161, *S. erratus*, male palp, mesal; 162, *S. erratus*, male palp, ectal; 163, *S. erratus*, male carapace, lateral; 164, *S. erratus*, epigynum; 165, *S. erratus*, internal genitalia, ventral; 166, *S. monicus*, male carapace, lateral; 167, *S. erratus*, male palpal organ, anterio-mesal, ED removed; 168, *S. erratus*, male palpal tibia, dorsal; 169, *S. monicus*, male palpal tibia, dorsal. Abbreviations: M, membranous apophysis; SA, suprategular apophysis (Scale lines 0.1 mm, except Figs. 163, 166, 0.2 mm).

epigastric plates); from these three species *S. fasciatus* is readily separated by the epigynum (Fig. 155 cf. Figs. 142, 127, 164). *S. fasciatus* is very close to *S. novellus* in both sexes; the chief distinction lies in the presence in *S. novellus* of clear epigastric striae, and the male carapace lobes are different (Fig. 154 cf. Fig. 153). There are also small differences in the palpal organs and in the epigyna (Fig. 155 cf. Fig. 156).

Distribution.—All the records are from California (Map 4).

Natural History.—The males have been taken in December, the females in January - June and in December. There is no information on habitat.

Spirembolus novellus, new species

Figures 151, 152, 153, 156, 158, 160; Map 4

Holotype.—Male holotype from Pinnacles National Monument, California, February 23, 1956 (G. A. March); deposited in AMNH.

Description.—Total length: female 1.75 mm, male 1.35 mm. Carapace: length: female and male 0.60 mm. Brown, with blackish margins. Male carapace raised into large lobe (Fig. 153). Abdomen: black, with white bars/chevrons dorsally, and a broad white chevron ventrally just anterior to spinners. Lung covers with striae in both sexes on epigastric plates, very closely spaced but rather weak in female, clear and closely spaced in male. Sternum: brown, suffused with black. Legs: brown. Tibial spines: female 2221, male 1111. Tml: female 0.42-0.45, male 0.41. Male palp: Figs. 151, 152, 158. The embolic coil is large in diameter. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 156, 160.

Diagnosis.—The patterned abdomen and the striated epigastric plates place this species with *S. erratus* (those specimens which have striae), *S. praelongus* and *S. pusillus*. In the male, the form of the carapace separates *S. novellus* from *S. erratus* and *S. praelongus* (Fig. 153 cf. Figs. 163, 166), and confirmation is given by the form of the palpal tibia (Fig. 158 cf. Figs. 168, 169). *S. novellus* male is readily separated from *S. pusillus* by the larger diameter of the embolic coil (Fig. 152 cf. Fig. 134) and by the closely spaced striae in *S. novellus*. In the female, the genitalia are quite distinct from those of the other three species (Figs. 156, 160 cf. Figs. 142, 146; 164, 165; 171, 172). *S. novellus* is very close to *S. fasciatus* in both sexes: see *S. fasciatus* diagnosis.

Distribution.—Recorded from two localities in California only (Map 4).

Natural History.—The only male was taken in February, females in February and May. Nothing is known on habitat.

Spirembolus erratus, new species

Figures 161, 162, 163, 164, 165, 167, 168; Map 4

Holotype.—Male holotype from Laguna Beach, Orange County, California, December 28, 1932 (W. Ivie); deposited in AMNH.

Description.—Total length: female 1.35-1.45 mm, male 1.25 mm. Carapace: length: female 0.55-0.60 mm, male 0.55 mm. Yellow to orange-brown, with dusky markings and margins. Male carapace raised into small lobe (Fig. 163) with a small hole and sulcus behind each pair of lateral eyes. Abdomen: black, with white chevrons/bars dorsally; ventrally black with a broad lateral white stripe. The male has clear striae on epigastric plates, closely spaced but rather weak; in the female the striae are either absent or very weak. Sternum: yellow, suffused with black. Legs: yellow-brown. Tibial spines: female

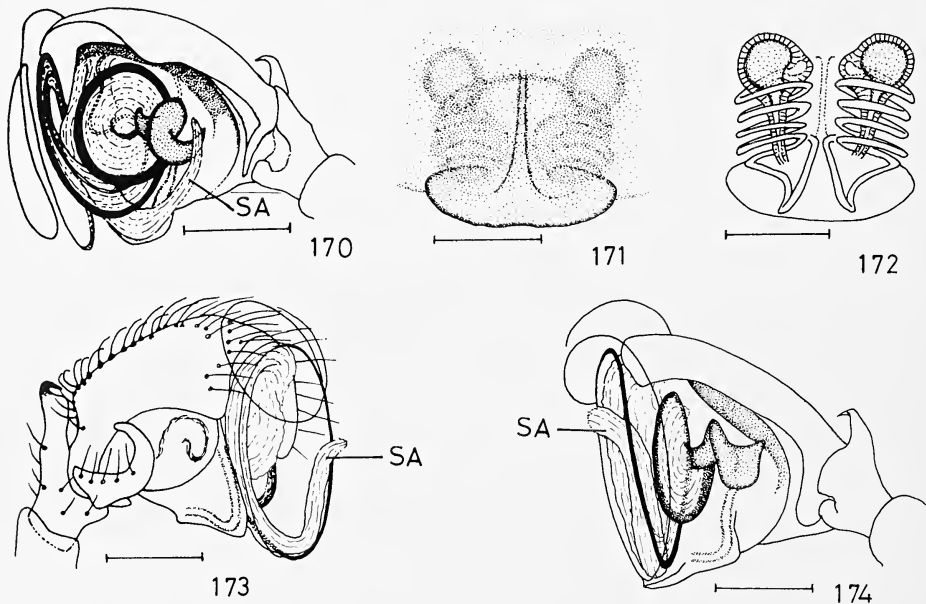
1111, male 0001, but weak in both sexes. TmI: female 0.37-0.40, male 0.35. Male palp: Figs. 161, 162, 168. The embolic coil is of large diameter. The palpal tibia is very similar to those of *S. monicus* and *S. praelongus*, and is somewhat different from the tibiae of the other species in the genus. Female palp: tibia with 2 trichobothria. Epigynum: Figs. 164, 165; the sperm duct forms a helix of several turns, a feature peculiar to *S. erratus*, *S. monicus* and *S. praelongus*.

No close relative of *S. erratus* having a unicolorous abdomen is known, but it seems probable that such a species may eventually be discovered.

Diagnosis.—The patterned abdomen and the striated epigastric plates group the male of this species with *S. novellus*, *S. pusillus* and *S. praelongus*. The form of the male carapace separates *S. erratus* from *S. novellus* and *S. pusillus* (Fig. 163 cf. Figs. 153, 137, 138, 140), and confirmation is given by the form of the palpal tibia (Fig. 168 cf. Figs. 158, 132) and by the palpal organs. The male of *S. erratus* is very similar to that of *S. praelongus*, being distinguished by the significantly larger diameter of the embolic coil in the latter (Fig. 161 cf. Fig. 174). In the female, the epigynum distinguishes *S. erratus* from all other species (except *S. praelongus*) which have a patterned abdomen. The epigyna of *S. erratus* and *S. praelongus* are very similar, but in the latter the spermathecae and ducts (partly visible through the integument) are more extended longitudinally and the spermathecae are rather smaller (Fig. 164 cf. Fig. 171).

Distribution.—Taken from a number of localities in California and from one locality in Nevada (Map 4).

Natural History.—Males have been taken in November, December, February and July (Nevada), females in all months except June, August, September and October. The main season of maturity may be in winter, at least in California. The only habitat recorded is in sycamore litter.



Figs. 170-174.—170, *S. monicus*, male palp, mesal; 171, *S. monicus*, epigynum; 172, *S. praelongus*, internal genitalia, ventral; 173, *S. praelongus*, male palp, ectal; 174, *S. praelongus*, male palp, mesal. Abbreviation: SA, supratregular apophysis (Scale lines 0.1 mm).

Spirembolus monicus (Chamberlin), new combination
Figures 166, 169, 170, 171; Map 4

Tortembolus monicus Chamberlin 1948: 558

Holotype.—Female holotype from Santa Monica, California, December 19, 1933 (W. Ivie); in AMNH, examined.

Description.—The male, which is described for the first time, was not taken in company with a female of *S. monicus*, but its characters indicate that it almost certainly belongs to this species. Total length: female 1.30 mm, male 1.0 mm. Carapace: length: female 0.55 mm, male 0.50 mm. Orange-brown, with dusky markings and margins. The male carapace rises steeply, with a small hole and sulcus behind the lateral eyes (Fig. 166). Abdomen: grey-black. Epigastric plates with striae, strong and quite widely spaced in male, weaker and less widely spaced in female. Sternum: yellow, suffused with black. Legs: pale orange-yellow. Tibial spines: lost from all specimens. TmI: female 0.35, male 0.33. Male palp: Figs. 169, 170; the embolus is very thin and hair-like distally, forming a coil of such wide diameter that the whole palpal organ appears slightly distorted on the mesal side. The SA is long, extending well onto the mesal side. Female palp: tibia with 2 trichobothria. Epigynum: Fig. 171; the outline of the ducts is sometimes indistinct. The internal genitalia are similar to those of *S. praelongus* (Fig. 172), the sperm duct forming a coil of several turns.

Diagnosis.—The unicolorous abdomen and the striated epigastric plates place this species with *S. demonologicus*. In the male these two species are readily separated by the palpal organs (Fig. 170 cf. Fig. 134) and by the carapace lobes, as well as by the considerable difference in size. The females of these two species are clearly separated by their epigyna (Fig. 171 cf. Figs 136, 139). *S. monicus* should not be confused with *S. praelongus*, which has closely similar sex organs but a patterned abdomen.

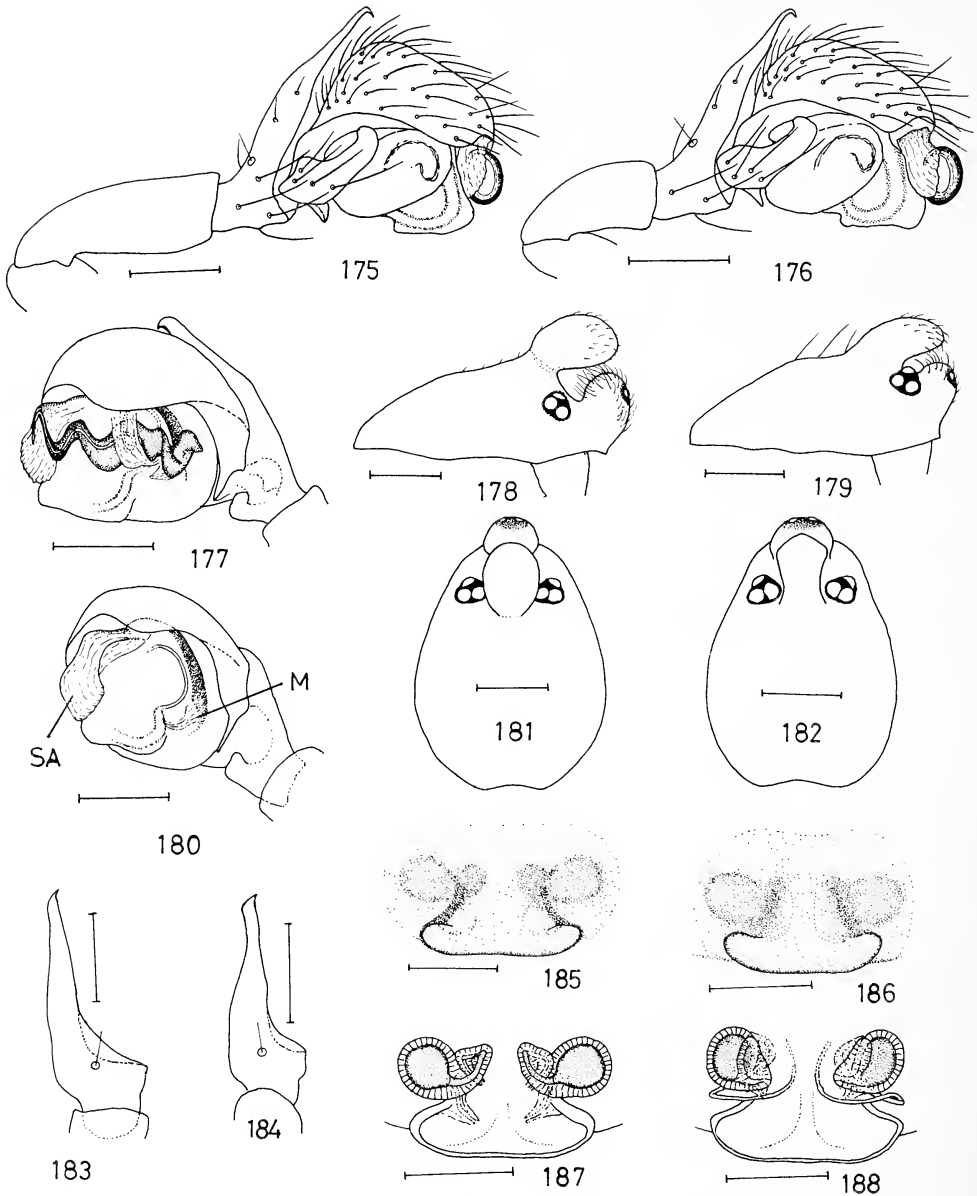
Distribution.—Known from three localities in California (Map 4).

Natural History.—The only male was taken in February, the females in December and January. The habitat was not recorded.

Spirembolus praelongus, new species
Figures 172, 173, 174; Map 4

Holotype.—Male holotype from Santa Monica, California, December 19, 1933 (W. Ivie); deposited in AMNH.

Description.—Total length: female 1.25-1.35 mm, male 1.10-1.15 mm. Carapace: length: female and male 0.50-0.55 mm. Yellow-brown, with dusky markings and margins. Male carapace similar to that of *S. monicus*. Abdomen: dorsally grey-black with clear white chevrons, the white markings extending to the ventral side. Epigastric plates with striae, strong and fairly widely spaced in male, weak and closely spaced in female. Sternum: yellow with dusky margins. Legs: yellow-brown. Tibial spines: female 1111, weak; missing in male. TmI: female 0.40, male 0.36. Male palp: Figs. 173, 174. The embolus is very thin and hair-like distally, forming a coil of large diameter. The SA is very long. Female palp: tibia with 2 trichobothria. Epigynum: similar to that of *S. monicus*, but the internal ducts are more clearly visible; the sperm duct (Fig. 172) forms a coil of several turns.



Figs. 175-188.—175, *S. bilobatus*, male palp, ectal; 176, *S. redondo*, male palp, ectal; 177, *S. bilobatus*, male palp, mesal; 178, *S. bilobatus*, male carapace, lateral; 179, *S. redondo*, male carapace, lateral; 180, *S. bilobatus*, male palpal organ, mesal, ED removed; 181, *S. bilobatus*, male carapace, dorsal; 182, *S. redondo*, male carapace, dorsal; 183, *S. bilobatus*, male palpal tibia, dorsal; 184, *S. redondo*, male palpal tibia, dorsal; 185, *S. bilobatus*, epigynum; 186, *S. redondo*, epigynum; 187, *S. bilobatus*, internal genitalia, ventral; 188, *S. redondo*, internal genitalia, ventral. Abbreviations: M, membranous apophysis; SA, suprategular apophysis (Scale lines 0.1 mm, except Figs. 178, 179, 181, 182, 0.2 mm).

S. praelongus is closely similar to *S. monicus*, the chief difference being the patterned abdomen.

Diagnosis.—From all other species with a patterned abdomen, *S. praelongus* is readily separated by the palp in the male and by the epigynum in the female. Confusion is possible only with *S. erratus*. The male of *S. praelongus* is distinguished quite easily from *S. erratus* by the larger diameter of the embolic coil (Fig. 174 cf. Fig. 161), but the females present more difficulty. The genitalia of the two species are very similar, but in *S. praelongus* the spermathecae are somewhat smaller and the internal organs are more extended longitudinally (Figs. 171, 172 cf. Figs. 164, 165). *S. praelongus* should not be confused with *S. monicus*, which is very similar apart from the unicolorous abdomen.

Distribution.—Known only from the type locality (Map 4). The four males and five females (holotype and paratypes) were taken at the same time and in the same locality as *S. monicus* and *S. erratus*; in the AMNH material these specimens were mixed with *S. erratus* in a vial labelled "*Tortembolus fasciatus*".

Natural History.—Both sexes were taken in December. Nothing was recorded on habitat.

Spirembolus bilobatus (Chamberlin and Ivie), new combination

Figures 175, 177, 178, 180, 181, 183, 185, 187; Map 4

Bactroceps bilobatus Chamberlin and Ivie 1945: 224

Holotype.—Male holotype from Pacific Grove, California, September 1, 1937 (W. Ivie); in AMNH, examined.

Description.—Total length: female 1.8-2.0 mm, male 1.5-1.7 mm. Carapace: length: female 0.85-0.90 mm, male 0.75-0.80 mm. Chestnut-brown, with dusky markings and margins. Male carapace raised into distinct lobes (Figs. 178, 181). Abdomen: grey to black. Sternum: brown, suffused fairly heavily with black. Legs: brown. Tibial spines: female 1111, male 0011. TmI: female and male 0.52-0.57. Male palp: Figs. 175, 177, 180, 183. The embolus is short and stout, in a small coil. Female palp: the number of trichobothria on the tibia is not constant, being 2 or 3 on either palp. Epigynum: Figs. 185, 187.

Diagnosis.—The male of *S. bilobatus* is recognizable at once by the form of the head, which is sufficiently distinct from that of *S. redondo* to make confusion unlikely (Figs. 178, 181 cf. Figs. 179, 182); confirmation is given by the palp, which is very similar to that of *S. redondo* but has the patella somewhat longer (Fig. 175 cf. Fig. 176). The female of *S. bilobatus* is distinguishable from most of the other species by the epigynum; only the epigyna of *S. redondo* and of *S. whitneyanus* could be confused with *S. bilobatus* (Fig. 185 cf. Figs. 186, 93), but distinction from these two species is given by the tibial spines (1111 in *S. bilobatus* female, 2221 in *S. redondo* and in *S. whitneyanus*.).

Distribution.—Known only from California (Map 4).

Natural History.—Numerous males and females have been taken in September, which seems to be the main period of maturity, and a female has also been found in December. The types were sifted from leaves from under shrubs at the edge of a sand dune (Pacific Grove, California).

Spirembolus redondo (Chamberlin and Ivie), new combination

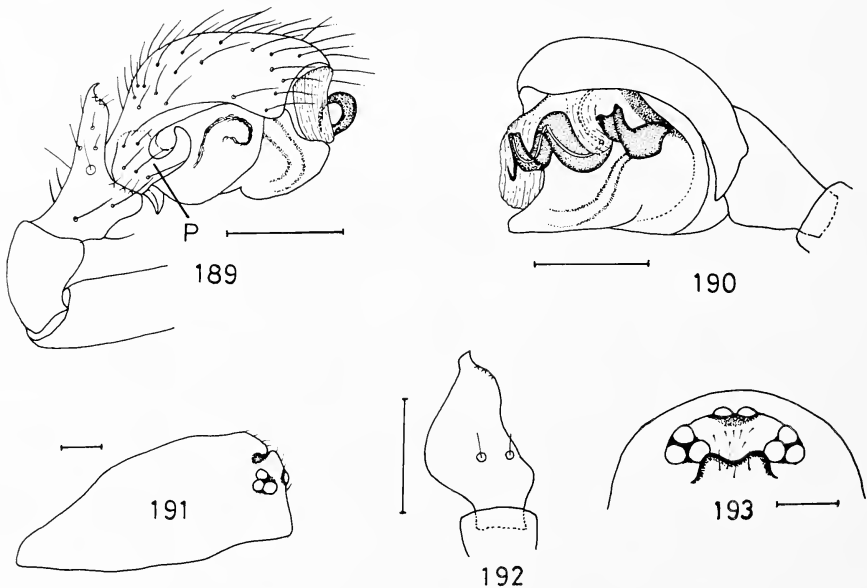
Figures 176, 179, 182, 184, 186, 188; Map 4

Bactroceps redondo Chamberlin and Ivie 1945: 225

Holotype.—Male holotype from 2 miles south of Redondo Beach, California, March 18, 1941 (W. Ivie); in AMNH, examined.

Description.—Total length: female 1.55-1.70 mm, male 1.35-1.50 mm. Carapace: length: female 0.70-0.75 mm, male 0.70 mm. Brown to deep brown, with dusky markings and margins. Male carapace raised into distinct lobes (Figs. 179, 182). Abdomen: grey to black. Sternum: brown, suffused with black. Legs: yellow to brown. Tibial spines: female 2221, male 0021. TmI: female 0.48-0.54, male 0.45-0.47. Male palp: Figs. 176, 184; palpal organs almost identical with those of *S. bilobatus*. Female palp: the number of trichobothria on the tibia is not constant, being 2 or 3 on either palp. Epigynum: Figs. 186, 188.

Diagnosis.—The male of *S. redondo* is recognizable at once by the form of the head, which is sufficiently distinct from that of *S. bilobatus* to make confusion unlikely (Figs. 179, 182 cf. Figs. 178, 181); confirmation is given by the palp, which has the patella relatively shorter than in *S. bilobatus* (Fig. 176 cf. Fig. 175). The female of *S. redondo* is distinguishable from most other species by the epigynum; only the epigyna of *S. bilobatus* and *S. whitneyanus* could be confused with *S. redondo* (Fig. 186 cf. Figs. 185, 93). *S. redondo* female is separable from *S. bilobatus* by the tibial spines (2221 in *S. redondo*, 1111 in *S. bilobatus*). The epigynum of *S. whitneyanus* though close is usually distinguishable, and these two species also show differences in the stoutness of the legs: e.g. tibia I 1/d is ca. 6 in *S. redondo* and 4-4.5 in *S. whitneyanus*.



Figs. 189-193.—189, *S. mirus*, male palp, ectal; 190, *S. mirus*, male palp, mesal; 191, *S. mirus*, male carapace, lateral; 192, *S. mirus*, male palpal tibia, dorsal; 193, *S. mirus*, anterior of male carapace, dorsal. Abbreviation: P, paracymbium (Scale lines 0.1 mm).

Distribution.—Known only from California (Map 4).

Natural History.—Males have been taken in March, September and October, females in January, March, April, September, October, November and December. The main period of maturity is probably in autumn and winter. The types were sifted from leaves taken under shrubs.

Spirembolus mirus, new species
Figures 189, 190, 191, 192, 193; Map 4

Holotype.—Male holotype from 9 miles west of Bishop, California, May 12, 1959 (L. M. Smith); deposited in AMNH.

Description.—Only the male is known. Total length: male 1.50 mm. Carapace: length: male 0.70 mm. Brown; there is a small lobe behind the eyes, and a hole behind the lateral eyes (Figs. 191, 193). Abdomen: grey. Eyes: in a *Pholcomma*-like arrangement (Fig. 193). Sternum: pale yellow. Legs: pale brown to brown. Tibial spines: male 0011. Tml: male 0.35-0.40. Male palp: Figs. 189, 190, 192. Embolus short and stout, in a small coil.

Diagnosis.—This species is recognizable at once in the male by the small lobe behind the eyes, coupled with the form of the palp.

Distribution.—Known only from the holotype and two paratype males (Map 4).

Natural History.—The males were taken in May. Nothing was recorded on habitat.

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THE PREDATORY BEHAVIOR OF *CYRTOPHORA* (ARANEAE: ARANEIDAE)

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ABSTRACT

Units of predatory behavior, described in four species of *Cyrtophora*, include resting positions, jerking and tensing of the web, web shaking, prey immobilization, cutting and pulling out, transportation to the hub and manipulation of the prey at the hub. With the exception of web-shaking behavior, all units of behavior are of the "advanced" type that occurs also in spiders of the genera *Argiope*, *Araneus* and *Eriophora*. Four different attack sequences are given to different prey types. Two of these involve immobilization by biting and two immobilization by wrapping. Prey are transported to the hub either on a silk thread or in the chelicerae. The predatory behavior of *Cyrtophora* differs from that of *Argiope* and *Eriophora* in the following respects: (a) the spider does not maintain dragline connection with the hub, (b) immobilization wrapping is generally restricted to beetles, pentatomid bugs, and large insects, (c) prey are never left in the web after immobilization, but always carried immediately to the hub, and (d) "Rundgang" behavior, involving multiple attachments of wrapped prey to the hub, was not observed. I suggest that *Cyrtophora* has evolved from an *Argiope*-like araneid in which prey immobilization by wrapping already existed. The modifications of this advanced-type predatory behavior can be related to the specialized web of *Cyrtophora*.

INTRODUCTION

Spiders of the genus *Cyrtophora* (Araneidae) have a specialized orb web (Kullmann 1958, 1959, Lubin 1972, 1973, Blanke 1972) which consists of a nonsticky horizontal sheet with an irregular barrier web above and below, also made of nonsticky silk (see Lubin 1973: Fig. 1). The sheet is a fine-meshed orb web, composed of radii and a nonadhesive structural spiral, but lacking the typical araneid viscid spiral. Directly below the sheet is a "free space" with few thread attachments to the sheet's undersurface. The "hub" of the orb is open, of irregular shape and variable in size. I have argued that because *Cyrtophora* webs are strong, durable and infrequently renewed, they are therefore well adapted to open habitats where they are exposed to heavy rains and/or strong winds (Lubin 1973).

It seemed probable that the specialized web of *Cyrtophora* would be associated with some interesting modifications of the spider's prey-capture behavior since an effective attack through a close-meshed sheet presents different mechanical problems compared to attacks in ordinary orbs. On the other hand, it has been shown that prey-capture

behaviors of araneids are relatively conservative within genera and similar patterns often occur in closely related genera (Robinson 1975). Since the taxonomic affinities of *Cyrtophora* within the Araneidae are obscure (Kaston 1964, Kullmann 1958, Blanke 1972), I felt that a study of predatory behavior might shed some light on the relationship of this genus to other araneids.

The study concentrated mainly on the functions and variability of predatory behavior patterns within the genus *Cyrtophora*. Mechanisms, or causation, and adaptive values of these behaviors were not tested in most cases and are, therefore, largely speculative. General knowledge of the biology of these spiders (Lubin 1972, 1973, 1974) and detailed studies of the prey of *C. moluccensis* in nature (Lubin, unpublished) have aided in interpreting the functions of the predatory behavior patterns.

Robinson and Olazarri (1971) divided the prey-capture behavior of araneid spiders into five functional stages: (1) detection and location of prey, (2) discrimination of prey type, (3) prey immobilization, (4) transportation of prey to the feeding site, and (5) manipulation of prey and feeding. I have emphasized the patterns of prey immobilization and transport to the hub, as a great deal of variation occurs in these behaviors. The behaviors associated with prey detection and location and discrimination of prey type are not easily discerned; these aspects are treated less thoroughly.

MATERIALS AND METHODS

Four species of *Cyrtophora* were studied during 1970-71: *C. citricola*, *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Details of size, habitat and study locations of these species are given in Table 1 and Lubin 1973, 1974. All species concerned have similar web structure. *Cyrtophora monulfi* has, in addition to the web, a conical, silken retreat above the hub, where it rests during the day (Lubin 1974: Plate 3). *Cyrtophora citricola* occasionally builds a retreat of dead leaves in the upper barrier web above the hub (Kullmann 1958, Blanke 1972). All investigations on *C. citricola*, *C. monulfi* and *C. moluccensis* were performed on field populations. *Cyrtophora cylindroides* were collected in the field and tested in the laboratory.

Live insects of various types were presented individually to adult female spiders. Insects tested were blowflies (Calliphoridae), fruitflies (*Drosophila* sp.), stratiomyid flies, moths and butterflies, katydids (Tettigoniidae), grasshoppers (Acrididae and Tetrigidae), dragonflies, pentatomid bugs, large scarab beetles (Melolonthinae), and weevils (Curculionidae). In most cases, with the exception of moths, butterflies and grasshoppers, insects within a category were of the same species. A weight range was established for each category of prey (Table 2). All insects tested on *C. moluccensis*, *C. cylindroides* and *C. citricola* came from habitats in which the spiders themselves were found. The natural prey of *C. moluccensis* included insects from all the above categories (Lubin, unpublished). The insects tested on *C. monulfi* were probably less representative of its natural prey, which may be restricted to small grassland insects.

In testing spiders with various insects, I alternated the different types of prey, and in no case was a spider tested with more than one prey per day. However, with the exception of the caged *C. cylindroides*, I had no record of the previous prey of the experimental animals. Some of the variation observed in predatory responses may have been due to differences in levels of hunger or previous experiences of these spiders.

Table 1.—Study sites, habitats, and sizes of four species of *Cyrtophora*.

Species	Length (mm)	Weight (mg) ± SD	Study Sites	Habitat	Habits
<i>C. citricola</i> (Forskall)	15 (Levi and Levi, 1968)	No data	Near Legon, Ghana ORSTOM Botanical Garden, Tananarive, Malagasy Republic Lamto, Ivory Coast	Roadside and wooded savanna Cacti and ornamental shrubs, fences,	Colonies, occasionally solitary. Same
<i>C. moluccensis</i> (Doleschall)	20-28 (Chrysanthus, 1959)	1163±415 n = 33	Wau and Bulolo, Morobe Province, Papua New Guinea	Wooded savanna Clearings and areas of human habitation: fences, electricity wires, ornamental trees and shrubs; roadside vegetation, forest edge.	Same Colonies, occasionally solitary.
<i>C. cylindroides</i> (Walckenaer)	15 (Chrysanthus, 1959)	326±14 n = 27	Lae, Bulolo, Morobe Province, Papua New Guinea	<i>Araucaria</i> plantations, lowland rainforest to 1000m elev.	Solitary
<i>C. monulfi</i> (Chrysanthus)	8-10	58±15 n = 10	Wau, Lae, Morobe Province, Papua New Guinea	"Kunal" (<i>Imperata</i> spp.) grassland, roadside vegetation, fences and ornamental shrubs.	Solitary or aggregations

Prey-capture behaviors were analyzed in terms of functional units. Commonly occurring sequences of these behavior units were established for each of the four species. Prey-capture sequences and durations of behavior units within a sequence were recorded for each prey-capture incident. Super-8 mm films were made of predatory sequences of *C. moluccensis*, *C. cylindroides*, and *C. monulfi* with a variety of prey. Descriptions of behavior units are based partly on analyses of these films, and partly on direct observation. The terminology and methods of description and analysis of behavior sequences are similar to those used by Robinson and Olazarri (1971). Whenever possible, I have compared behavior units and sequences of prey-capture behaviors of *Cyrtophora* with those of other orb weavers.

CYRTOPHORA PREDATORY BEHAVIOR

The general description of the prey-capture behavior of *Cyrtophora* given below is based mainly on the behavior of the three larger species: *C. moluccensis*, *C. citricola* and *C. cylindroides*. Differences in behavior between the four species studied are detailed later.

The spider rests at the hub or in the retreat (*C. monulfi*). An airborne insect striking the upper barrier web either drops onto the horizontal net or remains entangled in the upper barrier web. The prey produces vibrations in the web upon impact and/or during struggling (Suter 1978), and these are transmitted via web elements to the hub (Walcott 1963). Some discrimination of prey characteristics on the basis of vibration frequencies may occur at this stage (Walcott and Van der Kloot 1959, Robinson and Olazarri 1977), although accurate discrimination of prey type is unlikely (Suter 1978). Location of prey in the web often involves pulling and jerking the net or threads of the upper barrier web with legs I (the spider's four pairs of legs are numbered here I-IV from front to rear).

If the prey falls on the net, the spider runs out to it along the undersurface and, in many instances, touches it with legs I and/or with the palps before attacking. Chemo-receptors and tactile receptors abound on the tarsi and palps of araneid spiders (Foelix 1970a, 1970b), suggesting that discrimination of prey type may occur at this stage as well. Peters (1933) and Robinson (1969) obtained evidence for tactile discrimination at this stage by showing that both *Araneus diadematus* and *Argiope argentata* could distinguish between lepidopterans and other insects after touching them with the legs and palps.

Insects are immobilized by biting or by wrapping in silk, or by a combination of the two methods. If an insect remains caught in the upper barrier web, the spider runs out under the sheet and shakes it violently until the prey falls on the sheet. Insects that cannot be dislodged in this manner are attacked and immobilized in the upper barrier web. The barrier web may be reached by climbing through the open hub, climbing over the outer edge of the sheet, or by cutting a hole in the sheet and climbing through it. Insects are rarely attacked in the lower barrier web.

After immobilization, prey are pulled out or cut out of the sheet or barrier web with the chelicerae. Post-immobilization wrapping at the capture site, and/or biting and manipulation of prey in the chelicerae may occur at this stage. In some instances, the spider rests under or near the prey and cleans its palps, chelicerae and legs prior to transporting the prey to the hub. Prey are carried to the hub on the undersurface of the net in the spider's chelicerae, or dangling from the spinnerets on a silk thread.

Prey carried to the hub on silk are generally suspended at the hub by a thread, or wrapped (post-immobilization wrap at the feeding site) and suspended. Insects that are carried in the jaws are retained in the jaws, or wrapped and suspended at the hub. Pre-feeding manipulation of prey and actual feeding occur at the hub.

As noted previously by Kullmann (1958), *Cyrtophora* species do not leave a dragline behind them while moving under the sheet. This is unlike all other araneids, which maintain dragline connection with the hub during prey capture.

DESCRIPTION OF BEHAVIOR UNITS

Resting Positions

Several resting positions occur in the species studied.

Rest under hub.—The spider rests under the hub, with all legs in contact with the horizontal net. *Cyrtophora cylindroides* always rests in this position, as do *C. moluccensis* and *C. citricola* individuals that lack egg sacs. *Cyrtophora citricola* and *C. moluccensis* females with recent egg sacs assume a modified rest-under-hub posture, in which legs IV touch the egg sacs (Figure 1). This position is assumed at night and during part of the

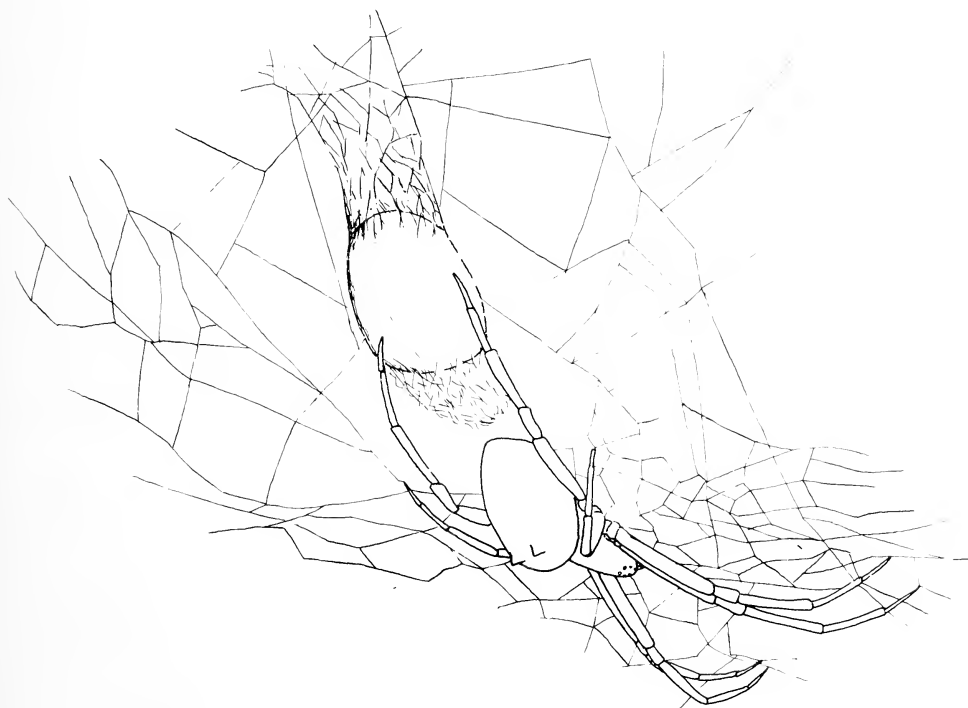


Fig. 1.—*Cyrtophora moluccensis* adult female with egg sac in rest-under-hub position. Note that legs IV are holding onto the egg sac while legs I and II are under the web in a position to monitor vibrations from the net.

day. When resting under the hub, the spider is in maximum contact with the horizontal net and is probably in the best position for receiving web vibrations.

When disturbed, *C. citricola* assumes a cryptic position which involves pulling all the legs inward toward the body, thereby obscuring the typical spider-like outline. Another small, unidentified species of *Cyrtophora* in New Guinea (sp. "D"), has a similar cryptic resting posture.

Cyrtophora monulfi leaves its retreat and rests under the hub at night, presumably when its predatory activity is most intense and/or when the danger from visually orienting predators is least.

Rest under egg sac.—*Cyrtophora citricola* and *C. moluccensis* females with egg sacs assume a resting posture under the egg sac throughout most of the day (Lubin 1974: Figure 2). In this position, the last two or three pairs of legs rest on the egg sac, while legs I or legs I and II touch the horizontal net or threads of the barrier web above the hub. Defense of egg sacs against diurnal parasites is important in *C. moluccensis* colonies (Lubin 1974) and contact with the egg sac is maximal in this position. The spider may, however, be less capable of receiving stimuli from prey in the web. *Cyrtophora cylindroides* females with egg sacs were never observed in this posture.

Rest in retreat.—Of the species studied, only *C. monulfi* consistently builds a retreat and rests in it during the day. The retreat is conical, with the open end facing downward toward the horizontal net, and is made entirely of silk. The spider can close off the open end of the retreat by pulling the lower edge inward with legs I (Figure 2). Normally, however, the retreat is open and the spider rests in it with legs I touching the threads of

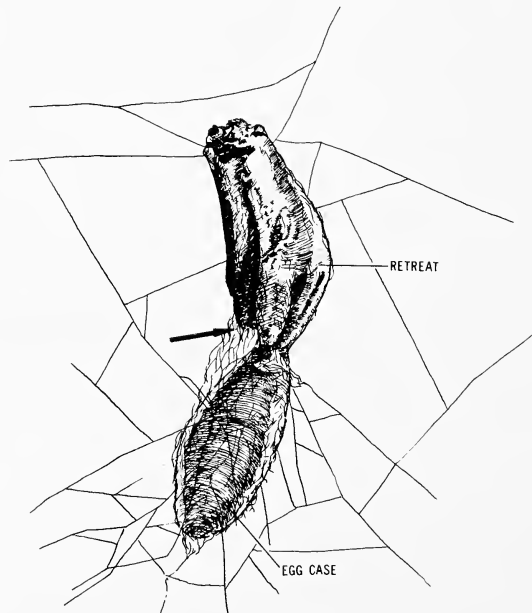


Fig. 2.—Conical silk retreat of *C. monulfi* adult female with egg sac attached to the lower edge. The spider closes off the mouth of the retreat by pulling the lower lip inward with the first pair of legs. Arrow points to lip of retreat.

Table 2.—Comparison of attack and immobilization sequences with different types of prey in 4 species of *Cyrtophora*. Frequency of occurrence, in percent, of the different sequences are shown after each sequence. n = sample size. Weight ranges of prey are, in mg: Lepidoptera 25-150 (*C. moluccensis*), 50-150 (*C. cylindroides*), 15-100 (*C. monulfi*); fruitflies c. 15; blowflies 50-60; stratiomyid flies 100-120; orthopterans 100-175 (*C. moluccensis*, *C. cylindroides*), 12-15 (*C. monulfi*); dragonflies c. 150; scarab beetles 500-1000; weevils c. 35; pentatomid bugs c. 35. Prey given to *C. citricola* were not weighed, but were similar in size to prey given to *C. cylindroides*. (A = modified sequence, see text.)

Attack sequences							
Prey type	<i>C. moluccensis</i>		<i>C. citricola</i>		<i>C. cylindroides</i>		<i>C. monulfi</i>
Lepidoptera	bite/wrap	83	bite/wrap	81	bite/wrap	90	bite/wrap 100
	bite	8	bite	9	bite	5	
	wrap/bite	8	wrap/bite	5	wrap/bite	5	
			wrap	5			
Blowflies	n = 24		n = 21		n = 20		n = 25
	bite/wrap	76	bite/wrap	91	bite/wrap	77	bite/wrap 100
	bite	20	bite	5	bite	14	
	wrap	4	wrap/bite	5	wrap/bite	9	
Stratiomyid flies	n = 25		n = 22		n = 22		n = 25
	wrap/bite	37					
	wrap	30					
	bite/wrap	30					
Fruitflies	other	3					
	n = 30						
			bite	100			
Orthopterans			n = 20				
	wrap	45	bite/wrap	42	bite/wrap	68	bite/wrap 59
	bite/wrap	31	wrap/bite	37	wrap/bite	16	wrap/bite 41
	wrap/bite	21	wrap	21	wrap	16	
Dragonflies	bite	3					
	n = 29		n = 19		n = 25		n = 22
	bite/wrap	58					
	wrap/bite	27					
Scarab beetles	wrap	15					
	n = 26						
	wrap/bite	92 ^A					
	wrap	8					
Weevils	n = 13						
	wrap	63					
	wrap/bite	32					
	other	5					
Pentatomid bugs	n = 19						
					wrap	85	
					bite/wrap	10	
					wrap/bite	5	
					n = 20		

the barrier web above the hub. The spider responds to vibrations in the web even when in its retreat. The egg sacs are suspended from the edge of the inner wall of the retreat and are well camouflaged (Figure 2).

Hang at hub.—During midday, when the sun is high individuals of *C. moluccensis* hang from the hub by legs IV, or III and IV (Figure 3). Spiders position themselves so that the dorsoposterior side receives the maximum insolation, while the rest of the body is shaded.

In this position the spider may be exposing a minimal surface area to the sun. When mirrors and shades were used to change the direction and angle of insolation, the spider reoriented to maintain its original position with regard to the "new" sun. These observations strongly suggest the presence of behavioral regulation of body temperature. Blanke (1972) observed this posture ("Hitzstellung II") in *C. citricola* when the spider was in direct sunlight at ambient temperatures above 31°C. Behavioral thermoregulation has been described in other web-building spiders, such as *Nephila clavipes* in Florida and Panama (Krakauer 1972, Robinson and Robinson 1974, 1978), *N. maculata* in New Guinea (Robinson and Robinson 1973), the linyphiid *Frontinella communis* (Pointing 1965), and a number of other araneid species (Robinson and Robinson 1978). Mechanisms for increasing heat loss or reducing heat gain by behavioral means occur commonly in terrestrial invertebrates that face repeated, high radiant heat loads. *Cyrtophora moluccensis*, with its typically exposed web, is most certainly included in this category.

Cyrtophora monulfi and *C. cylindroides* were not seen to hang from the hub. The white silk retreat of *C. monulfi* protects it from direct insolation, and may be an adaptation to the grassland habitat. *Cyrtophora cylindroides* is a shade-dwelling forest species and its webs never receive prolonged direct sunlight. The average midday temperature in a stand of 35-year-old *Araucaria cunninghamii* where *C. cylindroides* webs were found was considerably lower than in the surrounding open fields or at the plantation edge where *C. moluccensis* webs were located (R. Wiley, personal communication).

Cyrtophora moluccensis also assumes a hang-at-hub position during heavy rainfall. Unlike *N. maculata* (Robinson and Robinson 1973), *C. moluccensis* does not cut out

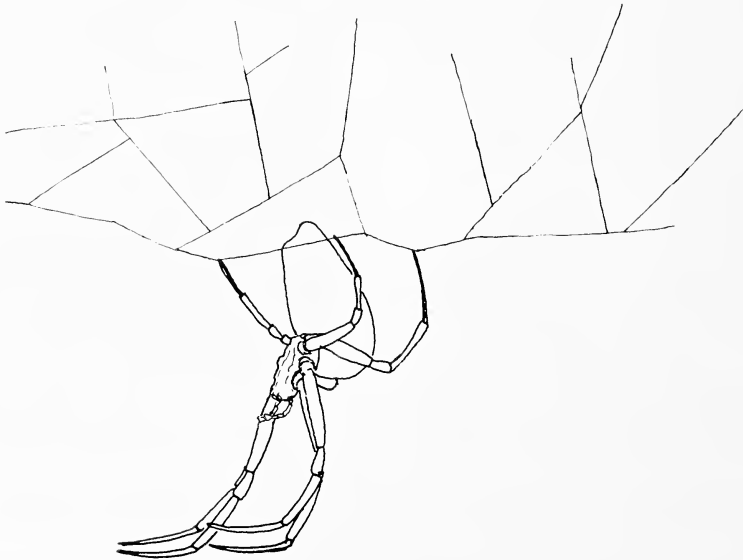


Fig. 3.—*Cyrtophora moluccensis* female hanging at the hub with legs III and IV in a sun-avoidance posture.

sections of its web during rain or move into the nearby vegetation. Presumably, by hanging at the hub, the spider presents a minimal surface to the rain, thereby reducing its impact. *Argiope argentata* was also observed to hang from the hub during heavy rain (Robinson and Robinson 1973) and it was suggested that the outstretched legs I and II act in the manner of a leaf drip-tip, enabling the water to flow off the spider's body. *Cyrtophora monulfi* does not hang at the hub in response to rain; data on *C. citricola* and *C. cylindroides* are unavailable.

Jerking

Jerking has been observed in all species studied (though not necessarily in all predatory sequences) and consists of a rapid pulling of the radii with legs I. [This was previously referred to as "plucking" (e.g., Robinson and Olazarri 1971) but Eberhard (pers. comm.) has pointed out that jerking more aptly describes the actual leg movements, since the force exerted on the radius is longitudinal to it rather than perpendicular.] The spider may jerk the web in response to movement in the web, or upon returning to the hub after a prey-capture sequence. In the latter case, the spider may turn in a circle at the hub, jerking the net at intervals as it turns. It may jerk threads of the upper barrier web as well. I also saw a low-intensity tensing of the web, in response to prey in the web. This involves slow pulling in the radii towards the body with legs I and II.

Jerking and web tensing may be a means of precise location of objects in the web. Due to the large number of radii and spiral connections in a *Cyrtophora* web, signal transmission may be somewhat diffuse. Jerking would put greater tension on the radii, and may also induce struggling in motionless prey, thereby enabling the spider at the hub to locate prey on the sheet. Robinson and Olazarri (1971) observed that *Argiope argentata* jerked the web move often when prey did not struggle and suggested that this is a method of accurately locating nonvibrating prey in the web. Earlier, Barrows (1915) proposed that radii in contact with prey would vibrate at a different frequency and that the spider could spatially compare the echo vibrations after jerking from unloaded and loaded radii. The mechanism of prey location by jerking deserves further investigation.

Like other araneids, *Cyrtophora* may also jerk the web as it approaches the prey. This probably allows for corrections in the spider's orientation toward nonvibrating prey. I have never observed *Cyrtophora* to "err" in the directional location of prey in the web. Occasionally, however, mistakes are made in distance location and the spider "overshoots the mark." This seems to occur most often with small, rapidly vibrating prey, such as buzzing blowflies, which elicit a very rapid attack [also observed in *Nephila maculata* (Robinson and Robinson 1973), and in the psechrid, *Fecenia* sp. (Robinson and Lubin, in press)].

A great deal of jerking takes place with prey trapped in the upper barrier web. Possibly signal transmission through the irregular barrier web is less accurate than through the net, making prey location more difficult.

Web Shaking

This involves sudden and large amplitude shaking of the horizontal net with legs I or legs I and II. Web shaking is quite distinct from jerking, involving a downward motion of the legs rather than the horizontal pull and release characteristic of jerking and tensing. Web shaking occurs in the context of both predatory and defensive behaviors:

- a. If an insect is caught in the upper barrier web, the spider runs out under the net until it is beneath the prey and shakes the net. This may be repeated many times until the prey is dislodged from the barrier web and drops onto the net.
- b. Web shaking occurs during intraspecific aggression (for example, during prey capture or web building) in *C. moluccensis* and *C. monulfi* (Lubin 1974).
- c. Theridiid kleptoparasites often approach a spider feeding at the hub, apparently in an attempt to steal prey. In such instances, the spider may shake the net at or near the hub, thereby chasing away the intruders.
- d. *Cyrtophora moluccensis* egg sacs are parasitized by a sarcophagid fly whose approach by flying through the barrier web elicits web shaking in adult *C. moluccensis* females (Lubin 1974). Parasite attacks have not been observed in other species of *Cyrtophora*.

Web shaking of the sort that I saw in *Cyrtophora* species does not seem to occur in other araneids, but does occur in *Pschrus argentatus* (Psecridae) which has a sheet-and-barrier web that acts as a knockdown trap like that of *Cyrtophora* (Robinson and Lubin, in press). *Nephila clavipes*, juvenile *N. maculata*, and *Argiope* and *Araneus* species vibrate their webs when disturbed by a large object, but these appear to be higher frequency vibrations whose functions may be to obscure the spider's outline (Tolbert 1975). *Metabus gravidus*, a colony-dwelling araneid from Costa Rica "bounces" on the web in response to an intruder (Buskirk 1975). It is possible that web shaking in *Cyrtophora* is derived from such antipredator web-vibrating or web-bouncing behavior.

Prey Immobilization

Biting.—Immobilization by biting occurs commonly in all species of *Cyrtophora* studied. The prey is initially grasped with legs I, II, and III, and the spider appears to bite the nearest or most readily accessible part of the insect's body. If this is a wing or a leg, the spider then moves down to a more "substantial" part of the insect's body, e.g., the base of an appendage, thorax or abdomen. Similar behavior occurs in other spiders, including *A. argentata* (Robinson and Olazarri 1971) and *Fecenia* sp. (Psecridae) (Robinson and Lubin, in press). Most prey are held in legs III, or II and III, during the bite. The duration of the bite varies: small insects are seized in the jaws and pulled out immediately, while larger prey may be bitten for several minutes (see below).

Prey that are immobilized by wrapping may be bitten after the wrap (post-immobilization bite at the capture site). The post-immobilization bite is generally directed toward the anterior portion of the insect's body, as is the case in *A. argentata* (Robinson and Olazarri 1971).

Prey with hard exoskeletons, such as most beetles, may be given a number of short bites during immobilization wrapping. These are probably exploratory bites, rather than actual penetration through the cuticle and injection of venom. The nocturnal araneid *Eriophora fuliginea* (Robinson et al. 1972) and *N. maculata* (Robinson and Robinson 1973) also repeatedly attempt to bite coleopterans. In both instances, the authors noted that penetration through the hard exoskeleton was unlikely and one could actually hear the clicking of the chelicerae as they glanced off the smooth elytra. *Cyrtophora* may also give short, exploratory bites to prey after removing it from the net, prior to transport to the hub. Rapid "bite and back off" sequences were not observed in *Cyrtophora*, though they are common in other araneids such as *Gasteracantha*, *Nephila*, and *Micrathena* (Robinson and Lubin, unpublished; Robinson and Robinson 1973).

Wrapping.—Prey are wrapped at several stages of the predatory sequence (Eberhard 1967, Robinson et al. 1969):

- a. Immobilization wrapping. Insects are attacked and partly or completely immobilized by wrapping in silk.
- b. Post-immobilization wrapping at the capture site. Prey that were immobilized by biting or by wrapping, are wrapped prior to transporation to the hub.
- c. Post-immobilization wrapping at the feeding site. Prey are wrapped at the hub prior to feeding.

In the wrap immobilization, *Cyrtophora* throws silk out under the sheet in broad swathes with legs IV. Often the spider approaches the prey and, turning 90° to 180°, faces away from the prey and begins throwing swathes of silk in an upward and slightly backward direction. Facing away and throwing behavior was observed most frequently in attack sequences on pentatomid bugs and large orthopterans presented to *C. moluccensis* and *C. cylindroides*. Similar behavior was observed in all species of *Argiope* studied, in *Araneus* spp. and, to a much greater extent in the nocturnal *Eriophora fuliginea* (see summary in Robinson 1975). In all wrap restraints, silk is initially thrown upwards from a distance. There is no actual bodily contact with the prey.

In *Cyrtophora*, initial throwing of silk does not always immobilize actively struggling prey. Silk swathes thrown upward onto the net may temporarily restrain prey by catching appendanges protruding through the net. The spider may then rapidly bite a hole in the net and resume throwing silk onto the prey as it drops through the hole. When the prey is thus partly immobilized, wrapping behavior changes gradually from throwing to the application of swathes of silk directly to the surface of the prey. Close contact wrapping is typical of wrapping after the initial restraint (post-immobilization wrapping).

Two phases of post-immobilization wrapping may be distinguished: wrapping of prey still caught on the net, and wrapping of prey hanging in the free zone beneath the net (free-wrapping). During the initial phase, the spider sits below the prey, holding it with legs II and III, while legs IV alternate in pulling out and applying swathes of silk directly onto the prey. In the case of insects restrained by biting, or wrapping and then biting, post-immobilization wrapping usually begins while the prey is still in the spider's jaws.

As the prey is freed from the net by pulling out or by cutting out, the first phase of wrapping merges into the second. The spider retains its hold on the net with one leg I (or with legs I and II) while grasping the prey with the remaining legs I, II, and III. The prey is suspended from the net by one or two threads. The spider is thus oriented perpendicular to the long axis of the prey and beings to rotate the prey with legs I, II and III and with the palps, while applying silk over the prey in a forward motion with legs IV. Legs I, II and III pull the anterior edge of the prey toward the spider's body, while legs IV push the posterior edge away from the body (see Robinson and Olazarri 1971:9). The prey is thus rotated toward the spider and silk is wound onto the prey. Free-wrapping also occurs in *A. argentata* (Robinson and Olazarri 1971) and in *E. fuliginea* (Robinson et al. 1972). The prey of *Argiope* and *Eriophora*, however, is supported on a radius of the orb web, while that of *Cyrtophora* hangs beneath the net. Like *Argiope*, *Cyrtophora* moves its abdomen in an arc from side to side as silk is pulled out with legs IV. In this manner, it covers the entire insect evenly with silk.

Large, bulky prey are wrapped in a manner that reduces their bulk. When wrapping dragonflies, for example, the wings and long abdomen of the dragonfly are pulled inward and wrapped together. The resulting prey package is of more manageable size and may be carried with less risk of entanglement in the web.

Post-immobilization wrapping may also occur at the hub, and during transport to the hub. Wrapping during transport occurs mainly when an insect becomes caught in the sheet or in the lower barrier web. Occasionally, insects that are transported in the jaws are wrapped partway to the hub and transferred to the spinnerets.

Insects that are restrained in the upper barrier web may be wrapped in the same manner as those immobilized on the net. A second wrapping generally occurs under the sheet (free-wrap), prior to transport to the hub.

Pulling Out and Cutting Out

Small prey may be pulled out of the sheet with the chelicerae. The spider pulls the prey down with the jaws and legs III, while legs I and II push up against the sheet. *Cyrtophora* attempts to pull out most prey that are bitten at the capture site (either immobilization or post-immobilization bite), including large prey that are subsequently cut out of the web. Pulling out seems to follow biting in the normal sequence of prey capture behavior, but is successful only with small, compact prey such as fruitflies and occasionally blowflies. Difficulty in pulling prey out of a *Cyrtophora* web is due to the strength and fineness of the mesh, rather than web adhesiveness, as in the case of typical orb weaver.

Pulling out in the jaws may also allow the spider to test the condition of an insect that has been immobilized by biting, without loosening the grip on it. Since insects do not actually adhere to the sheet, the possibility of escape from a *Cyrtophora* web due to incomplete immobilization is greater than from webs of other araneids (Lubin 1973). There would be an advantage, therefore, to testing prey immobility prior to releasing it for wrapping.

Most prey, other than very small insects, are removed from the sheet by a combination of alternately cutting out and pulling down with the legs and jaws. In cutting out, threads of the sheet or upper barrier web in immediate contact with the prey are cut, while the prey is pulled down with legs II and III, or I, II, and III. The functional distinction between cutting out and pulling out is less clear in *Cyrtophora* species than in *A. argentata* (Robinson and Olazarri 1971). Nor is there a definite temporal sequence of cutting spiral and radial web elements, as in *Argiope*. This is understandable, as there is no difference in physical properties between these elements in a *Cyrtophora* web. In all likelihood, the combination of cutting and pulling is simply a method of freeing prey with the minimum amount of damage to the sheet. Pulling out results in the least damage; cutting and pulling out results in a small hole, approximately the diameter of the insect as it is pulled through the sheet head first.

With insects that are immobilized entirely by wrapping, cutting out occurs as part of the wrap sequence, during the transition from restraint wrapping to free wrapping under the sheet.

Transportation to the Hub

Carry in jaws.—Small prey are often carried to the hub in the chelicerae. An insect may be wrapped at the capture site and transferred to the jaws for transport, retaining a swathe of silk connecting it to the spider's spinnerets. Small prey that are seized and pulled out with the jaws are generally carried to the hub in the jaws without prior wrapping.

Carry on silk.—Most prey are carried to the hub dangling on a thread from the spinnerets held by one or both legs IV. The spider's abdomen is oriented horizontally

under the net, and the wrapped prey package hangs down over the posterior edge of the abdomen. Holding with legs IV may prevent the insect from swinging from side to side and becoming entangled in the lower barrier web. *Araneus diadematus*, *Argiope argentata*, and *Nephila clavipes* also support either the prey package or the thread from which it is suspended, with legs IV (Peters 1931, Robinson and Olazarri 1971, Robinson and Mirick 1971), although *A. argentata* sometimes carries prey without support.

All prey, whether carried on silk or in the jaws, are transported to the hub on the undersurface of the sheet. *Cyrtophora* carries all prey to the hub and does not leave wrapped insects in the web at the capture site.

Manipulation and Feeding at the Hub

Prey carried on silk are suspended at the hub. Upon reaching the hub, the spider pulls down on the thread from which the prey is suspended with one leg IV, thus pulling out a length of thread, and then dabs the spinnerets onto the net. The spider then turns 180° and pulls the prey up to the chelicerae with legs I and II. The silk line is severed in the act of dabbing the spinnerets to the sheet, though the mechanism for this is not understood. As yet, no evidence of a cut-off valve has been found in araneid spinnerets (Wilson 1969).

Prey are manipulated with the palps, chelicerae, and legs I and II prior to feeding. Feeding generally occurs at the anterior end of the prey. During feeding, most prey are held in the jaws alone, and the spider resumes a resting position with all legs under the web. Large prey may be held with legs III; occasionally, *Cyrtophora* feeds in a hanging position with legs I, II, and III grasping the prey and legs IV holding onto the hub. The latter position undoubtedly reduces the spider's ability to receive web vibrations.

DESCRIPTION AND ANALYSIS OF BEHAVIOR SEQUENCES

Attack Sequences

Attack sequence is used here to denote prey immobilization and subsequent behavior up to transportation of the prey to the feeding site. Analysis of *Cyrtophora* prey capture sequences with various types of insect prey revealed four basic attack sequences: (1) wrap/bite/pull out or cut out/free-wrap, (2) wrap/cut out/free-wrap, (3) bite/wrap/cut out/free-wrap, and (4) bite/pull out (or cut out). Two of these sequences involve immobilization by wrapping, and two immobilization by biting. Table 2 shows the frequency of occurrence of each attack strategy in four species of *Cyrtophora* with different insect prey. Tables 3-5 give the durations of behavior units within sequences for *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Durations are given only for the most commonly occurring sequences with each prey type.

Post-Attack Sequences

Post-attack sequences involve transportation of prey to the hub and manipulation at the hub prior to feeding. The two basic methods of transportation, carry in jaws and carry on silk, have already been described. Frequencies of occurrence of these two methods in behavior sequences with different prey types are shown in Fig. 4. Durations of post-attack sequences and total sequence durations are shown in Tables 3 to 5.

The following discussion will concentrate on the variation in sequences of attack and transportation that occur with different prey and their possible adaptive values.

Table 3.—Duration of attack and transportation to hub and total durations of commonly occurring prey capture sequences in *C. moluccensis*. Total sequence durations represent the time from initiation of an attack to suspending the prey at the hub; manipulation of prey at the hub and feeding are not included. Not all behavior units were timed in each sequence; thus, sample sizes vary for each behavior category.

n = number of prey for which behavior was timed; M = mean duration, in seconds; SD = 1 standard deviation.

(A = Durations of wrap and cut out/free wrap were lumped together; B = wrap attacks that were too short to measure accurately are designated as 1 second duration; C = test-bites and manipulation of prey with legs and jaws; D = sequence repeated several times).

Prey and attack sequence		Attack		Transport		Total sequence
		Wrap	Bite	Cut out/free wrap	Carry to hub	
Moths (bite/wrap)	n		16	15	12	16
	M		75.1	47.5	20.3	109.6
	SD		85.1	21.3	30.5	111.9
	Range		6–265	21–90	5–116	50–340
Blowflies (bite/wrap)	n		18	16	14	18
	M		36.1	22.7	7.6	112.5
	SD		31.5	8.3	3.0	101.2
	Range		5–130	12–39	3–13	32–377
Stratiomyids (wrap/bite)	n	10	10	9	7	10
	M	8.6	109.9	52.2	11.6	185.0
	SD	5.8	61.6	14.5	10.95	104.5
	Range	2–17	3–219	7–55	5–36	77–412
Stratiomyids (wrap)	n	9 ^A			6	9
	M	56.1			9.5	96.4
	SD	44.5			8.5	62.2
	Range	15–136			3–25	22–201
Stratiomyids (bite/wrap)	n		9	9	5	9
	M		76.2	21.9	9.6	117.1
	SD		49.7	7.0	4.3	58.6
	Range		8–156	12–36	4–15	46–218
Grasshoppers and katydids (wrap/bite)	n	6 ^B	6	4	2	3
	M	13.5	54.2	37.0	6.5	195.3
	SD	16.8	76.6	10.4	2.1	115.3
	Range	1–38	2–207	24–49	5–8	69–295
Grasshoppers and katydids (wrap)	n	10 ^A			6	10
	M	40.0			28.3	101.1
	SD	14.95			28.8	88.7
	Range	22–58			9–75	53–323
Grasshoppers and katydids (bite/wrap)	n		5	5	5	5
	M		27.0	35.0	5.0	128.2
	SD		19.3	7.1	1.9	54.8
	Range		7–55	28–44	3–8	72–191
Dragonflies (wrap/bite)	n	7 ^B	7	7	7	7
	M	10.7	106.6	57.6	12.4	282.4
	SD	13.1	152.4	10.5	6.1	217.1
	Range	1–37	1–448	50–78	4–23	128–765
Dragonflies (bite/wrap)	n		14	14	12	14
	M		135.0	51.8	14.9	330.1
	SD		138.0	35.0	12.4	149.8
	Range		12–334	16–138	4–40	119–600

Table 3.—continued.

Weevils	n	6	6	3	2	6
(wrap/bites) ^C	M	16.8	56.5	16.3	4.5	117.2
	SD	7.6	70.0	14.4		53.7
	Range	9–28	1–184	8–33	3–6	60–202
Weevils	n	12 ^A			6	12
(Wrap)	M	12.45			12.3	56.6
	SD	3.1			13.5	34.6
	Range	8–19			2–36	20–123
Scarabs	n		12			12
(wrap/bites/	M		529.1			661.0
wrap) ^D	SD		374.0			357.2
	Range		57–1395			120–1400

Comparisons are made with the prey capture behaviors of *C. citricola* in Spain (Blanke 1972) and of other araneids.

Sequences With Moths.—Lepidoptera are nearly always immobilized by biting, by all four species of *Cyrtophora*. The third attack sequence, bite/wrap/cut out/free wrap, is the predominant one used with moths and butterflies. Robinson (1969) showed that *A. argentata* immobilizes moths by a long bite, while most other prey are restrained by wrapping. He suggested that since moths can escape readily from sticky webs by shedding the loose scales in contact with the web (Eisner *et al.* 1964), a rapid restraint by biting would be most advantageous. As the *Cyrtophora* web is nonsticky, scales can be of little advantage in freeing a moth from the web. It is more likely that a moth can slip out of the silk thrown on it during a wrapping attack and, therefore, the bite immobilization and immediate injection of venom is more effective. Robinson (1969) showed that Lepidoptera are recognized by the spider, at least in part, by their surface texture. Other araneids (e.g., *Eriophora fuliginea* and other *Argiope* spp.) which have sticky orbs and both wrap and bite immobilization behaviors, also use the biting restraint for Lepidoptera (Robinson 1975).

A small proportion of “mistakes”—moths attacked by a wrap immobilization sequence—was made by *C. citricola*, *C. cylindroides*, and *C. moluccensis*. This was found to be the case with *A. argentata* as well (Robinson 1969). Most of these mistakes were made with moths attacked in the upper barrier web. These moths were wrapped only a few times (2- to 3-seconds duration) and immediately bitten. It is possible that discrimination of prey type is more difficult in the barrier web, due to its diffuseness, than under the sheet. As moths make up a large fraction of the prey of *C. moluccensis* in the area studied (and possibly of the other species as well; Lubin, unpublished data), one might expect mistakes in the method of attack to be minimized. This appears to be the case: *C. moluccensis* made 8.3% mistakes with live moths, while *A. argentata* (which does not feed on lepidopterans to any large extent) made 17.2% mistakes with live moths and 16% mistakes with live butterflies (Robinson and Olazarri 1971). *Eriophora fuliginea*, a nocturnal araneid which may specialize on moths, attack-wrapped only 6% of the live moths (Robinson *et al.* 1972). These differences, while suggestive, are not statistically significant.

Most moths are wrapped at the capture site and carried to the hub on silk. The larger species, *C. moluccensis* and *C. citricola*, carry a small percentage in their jaws after a bite/pull out in jaws attack sequence. Some of these however, are wrapped part way to the hub and transferred to the spinnerets.

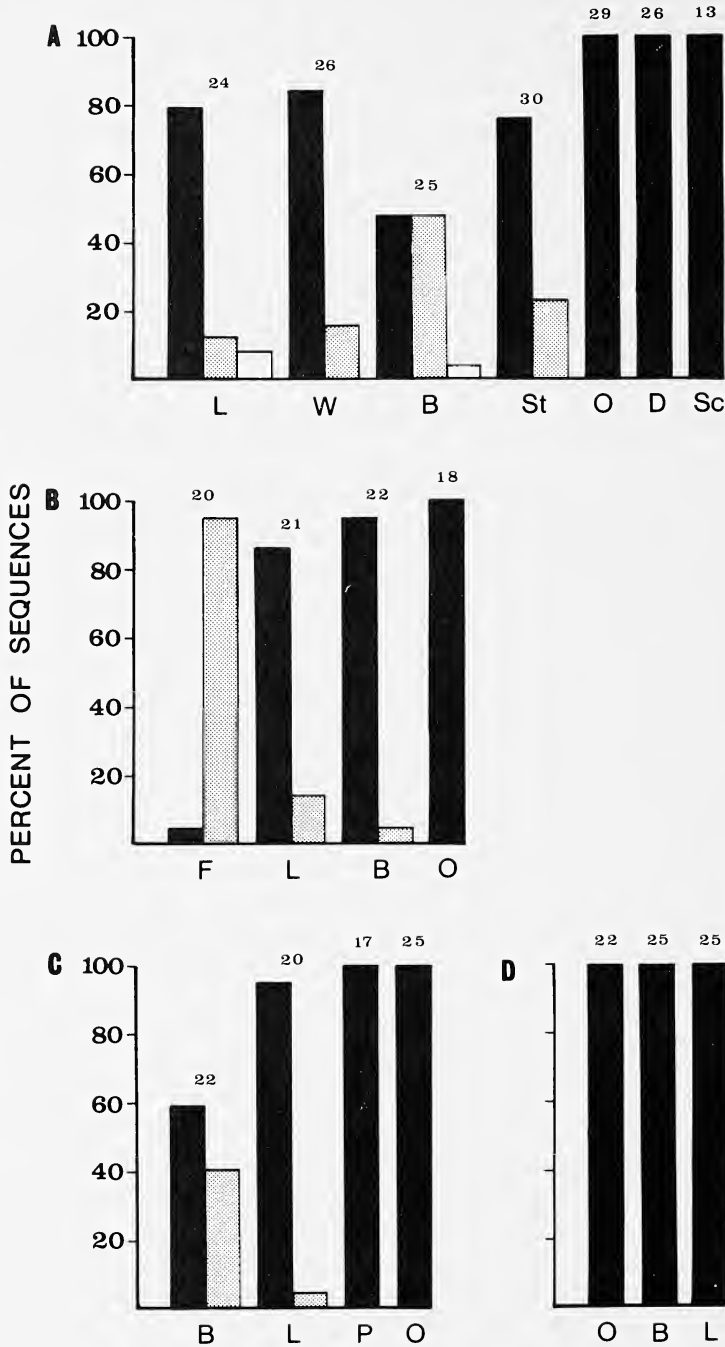


Fig. 4.—Frequency of occurrence, in percent, of transport to hub sequences in *C. moluccensis*, *C. citricola*, *C. cylindroides*, and *C. monulfi*. Transport sequences are: black bars = carry on silk, shaded bars = carry in jaws, white bars = carry in jaws and transfer to carry on silk. Numbers of trials are shown for each prey type. Prey types are: L=moths and butterflies, B=blowflies, St = stratiomyid flies, O = orthopterans (katydids, grasshoppers, pygmy grasshoppers), D = dragonflies, W = weevils, Sc = Scarab beetles, F = fruitflies.

Sequences With Flies.—Blowflies are immobilized predominantly by biting. Biting attacks were used on 96% of the blowflies tested on *C. moluccensis*, 90% of those tested on *C. citricola*, 100% of those tested on *C. monulfi*, and 95% of those tested on *C. cylindroides*. Small fruitflies tested on *C. citricola* were always immobilized by biting in a bite/pull out attack sequence (see also Blanke 1972:181). Blanke (1972) found that *C. citricola* attacked houseflies by biting.

Cyrtophora species attacked blowflies by biting even when the flies equalled or exceeded the weight of the spider (as in the case of blowflies given to *C. monulfi*). Wasp-mimicking stratiomyid flies (soldier flies), however, elicited 66.7% wrap restraints in *C. moluccensis*. *Cyrtophora* attacks most hymenopterans by wrapping (*C. citricola*: Blanke 1972; *C. moluccensis*; incidental observations). More than half of the wrap attacks on stratiomyids were of type I (wrap/bite), in which the wrap was of short duration (2 to 17 seconds), and was followed by a long bite not significantly different in duration from the bite given in a bite/wrap attack sequence. Possibly the spiders mistook the stratiomyids for wasps during the initial attack. One may postulate that the spider switches off the wrap attack as soon as it recognizes the prey to be nonhymenopteran. Recognition may occur only upon actual contact with the prey, after immobilization wrapping has begun. Since prey discrimination in orb weavers is based on tactile and chemosensory cues, the wasp mimicry of stratiomyids must extend to nonvisual characters, e.g., wingbeat frequency, for the spider to err in their recognition. Acoustical mimicry has, in fact, been described in a syrphid fly *Spilomyia hamifera* (Gaul 1952). Blanke (1972), however, found that *C. citricola* treated unidentified syrphid flies like other flies and immobilized them by biting.

Argiope argentata attacked 74% of live flies and 98% of live stingless bees (*Trigona* sp.) by wrapping (Robinson and Olazarri 1971). Peters (1931, 1933), however, found that vibrating flies were bitten by *Araneus diadematus*, and *Eriophora fuliginea* attacked most stingless bees by biting and pulling out (Robinson et al. 1972). The latter authors suggested that a biting attack is elicited by small, rapidly vibrating prey that have become trapped by only a few viscid spiral elements and may, therefore, easily escape. Since *E. fuliginea* has a coarser mesh web than *A. argentata*, stingless bees are held by fewer threads (often only one); this may explain the predominance of biting attacks in *E. fuliginea*. Because of its lack of sticky threads, the *Cyrtophora* web is relatively inefficient in restraining small, active insects (see evidence on blowfly escapes from *C. moluccensis* webs, Lubin 1973); hence, a rapid, biting attack would be most effective.

Transportation sequences with flies are variable (Fig. 4). Blowflies are carried entirely on silk by *C. monulfi* and predominantly on silk by *C. citricola* (95%) and *C. cylindroides* (59.1%). *Cyrtophora moluccensis* uses both methods with equal frequency. Stratiomyids, which are heavier than blowflies, are carried mainly on silk. Fruitflies, which are small and light, are not wrapped at the capture site and are carried in the jaws by *C. citricola*.

When fruitflies were tested in rapid succession, *C. citricola* attacked each additional fly while retaining the previous ones in the jaws, thus accumulating up to 5 fruitflies in the jaws. However, after 4-5 fruitflies had been accumulated, they were wrapped together into one prey package, and transferred to the spinnerets. Four to 5 fruitflies weigh approximately 40 to 50 mg, and are within the weight range of blowflies which are carried on silk by *C. citricola*. These observations imply that prey weight influences the mode of transportation to the hub in *Cyrtophora*. Other factors such as size and bulkiness of the prey may also be important.

Table 4.—Durations (in seconds) of attack and transportation to hub, and total durations of prey capture sequences in *C. cylindroides* (see Table 3). (A = this sequence was repeated several times.)

Prey and attack sequence		Attack		Transport		Total sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths (bite/wrap)	n		19	18	18	19
	M		290.2	55.9	10.0	414.7
	SD		187.1	19.3	3.1	180.7
	Range		46–764	23–83	4–15	189–844
Blowflies (bite/wrap)	n		17	17	16	17
	M		212.65	26.8	10.7	258.2
	SD		202.55	16.2	4.2	211.25
	Range		36–693	5–70	5–20	55–767
Katydid (wrap/bite)	n	3	3	3	3	3
	M	26.0	25.0	32.3	8.0	164.3
	SD	19.2	39.0	26.0	6.1	69.8
	Range	4–39	1–70	7–59	1–12	88–225
Katydid (wrap)	n	4		4	4	4
	M	29.25		49.5	12.0	179.75
	SD	11.7		58.4	4.3	141.5
	Range	14–42		16–137	8–18	76–377
Katydid (bite/wrap)	n		16	16	13	16
	M		48.6	54.0	12.7	241.4
	SD		43.2	37.4	6.8	84.2
	Range		6–151	5–127	4–30	85–381
Pentatomid (wrap/cut out/rest- clean) ^A	n	18			9	18
	M	161.7			11.1	281.2
	SD	115.1			4.9	171.5
	Range	29–383			6–20	44–577

Sequences with Orthopterans.—Orthopterans are immobilized either by biting or by wrapping. Although wrap restraints (sequences 1 and 2) occur more frequently in *C. moluccensis* and *C. citricola*, no one sequence predominates in all four species. It is significant that all three attack sequences involving both wrap and bite immobilization are commonly used on a single type of prey.

Argiope argentata wraps all crickets (Robinson and Olazarri 1971). Other *Argiope* species also wrap orthopterans (Robinson, B. and M. H. Robinson 1974). These authors have suggested that wrapping enables the spider to restrain dangerous prey while maintaining a safe distance from it. Species that do not attack prey by wrapping (e.g., *Nephila* spp., *Herrenia ornatissima*, *Micrathena* spp.) often restrain orthopterans and other large prey with a repeated bite/back-off sequence that is considerably less efficient than a wrap immobilization (Robinson et al. 1969, Robinson and Lubin, in press).

Since immobilization wrapping does occur in *Cyrtophora* species, why is it not used more frequently with orthopteran prey? There are perhaps two explanations. First, because of the strength and density of the horizontal orb web, *Cyrtophora* may be more protected from potentially dangerous prey than is *Argiope* (or any other typical orb-web spider). The horizontal sheet is always situated between the spider and its prey. Hence, the spider can “afford” to utilize a more direct bite immobilization, rather than wrapping

Table 5.—Durations (in seconds) of attack and transporation to hub, and total durations of prey capture sequences in *C. monulfi* (see Table 3).

Prey and attack sequence		Attack		Transport		Total sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths (bite/wrap)	n		25	25	20	25
	M		164.4	99.1	37.15	398.6
	SD		128.7	41.2	64.1	220.5
	Range		16–457	22–165	2–277	98–785
Blowflies (bite/wrap)	n		25	23	14	25
	M		118.2	56.0	14.0	245.7
	SD		108.9	23.2	8.9	124.1
	Range		28–545	14–107	3–32	111–626
Small grasshoppers (wrap/bite)	n	8	8	8	6	8
	M	5.4	30.0	27.0	5.0	155.9
	SD	4.9	18.55	7.7	3.2	110.3
	Range	1–16	1–59	11–36	2–11	94–423
Small grasshoppers (bite/wrap)	n		12	11	5	12
	M		79.75	38.9	4.2	184.7
	SD		92.5	18.0	1.9	109.5
	Range		17–333	17–73	2–7	40–437

from a distance. An analogy may be drawn between the methods of attack of *Cyrtophora* species and that of the sheetweb spider (Linyphiidae) or purse-web spider (Atypidae), both of which seize their prey in the jaws from a position of relative safety beneath a layer of silk. Second, since the horizontal sheet forms a barrier between the spider and its prey, it is difficult for *Cyrtophora* to completely immobilize prey by wrapping unless a large portion of the insect protrudes through the sheet into the thread-free zone. Katydidids are often not heavy enough or strong enough to break the sheet of a *Cyrtophora* web, and in such instances direct immobilization by biting may be more effective. Orthopterans that struggle and damage the sheet are immobilized entirely by wrapping. Many of the wrap/bite sequences given to orthopteran prey consist of a short-duration wrap and long-duration bite, as already observed with stratiomyid flies. Possibly the initial wrap attack is switched off upon some sort of feedback from the prey, e.g., prey harmless, or prey body not protruding through sheet. The predominance of biting attacks on blowflies may also be explained in this manner.

Predatory sequences initiated by immobilization wrapping in *A. argentata* were shorter than those initiated by biting (Robinson et al. 1969). It was suggested that another advantage to the spider of restraint wrapping was to minimize time spent away from the hub, the hub offering both protection and a central location for monitoring web vibrations. This seems particularly applicable to *Argiope* which returns to the hub after immobilization wrapping, leaving the prey in the web. *Cyrtophora* does not leave wrapped prey in the web. Furthermore, sequences in which prey are restrained by wrapping alone (sequence 2) are not significantly shorter in duration than sequences initiated by either bite/wrap or wrap/bite attacks (Tables 3 and 4), and the reduction in time spent away from the hub is not as pronounced as in *A. argentata*. Thus, the advantages of a wrapping attack may be more limited for *Cyrtophora* species.

Orthopterans were invariably carried to the hub on silk, though crickets of the same or greater weight than the orthopterans used here were carried in the jaws by *A. argentata* (Robinson 1969; *A. argentata* weighs approximately the same as *C. moluccensis*). The significance of this difference is unclear. It may be more difficult to carry heavy prey in the jaws under a horizontal orb web than under a near-vertical web.

Sequences with Dragonflies.—The dragonflies tested on *C. moluccensis* weighed approximately the same as the katydids, and the observed predatory sequences were similar to those with katydids as prey. The hypothesis proposed to explain the occurrence of all three sequences with orthopteran prey may be applied to dragonflies as well. Dragonflies were given a significantly longer bite than were katydids, whether it be an immobilization bite ($t = 1.65$, $p = 0.05$) or post-immobilization bite ($t = 1.80$, $p < 0.05$). Thus, the duration of the bite does not appear to be weight dependent, but may be related to other factors such as intensity of struggling of the prey or prey shape.

Dragonflies, like grasshoppers and katydids, were carried to the hub on silk.

Sequences with Beetles.—Small weevils (ca. 35 mg) and large scarabid beetles (500 to 1000 mg) were tested on *C. moluccensis*. All beetles were immobilized by wrapping. Attack sequence 2, wrap/cut out/free wrap, was used on most weevils. About 30%, however, were given short, exploratory bites after the initial wrapping restraint. This method of attack seems to be a variation on the typical wrap/bite sequence, where a series of short test-bites replace the long bite normally given to non-coleopteran prey. Half of the weevils that were bitten were carried to the hub in the jaws, and half were wrapped again and transferred to the spinnerets. In this instance, carrying on silk is perhaps influenced by the smooth surface of the beetle rather than by weight.

The attack sequence with large scarabs (*Melolontha* sp.) is a more complex variation of sequence 1, involving the behaviors wrap/attach thread to sheet (or hub)/test-bites/wrap, which may be repeated several times. A typical attack sequence on *Melolontha*, taken from field notes, is as follows:

Spider at hub. Moves to prey under sheet. Touch prey with palps and legs. Wrap (throw silk swathes under prey). Cut out with jaws while wrapping. Attach thread to sheet with spinnerets. Wrap (move over surface of prey). Begin rotating prey while wrapping (rotate-wrap). Test-bites. Rotate-wrap. Attach thread to sheet near hub. Test-bites. Rotate-wrap. Attach thread to sheet. Test-bites. Rotate-wrap. Cut proximal thread to sheet and attach thread closer to hub. Turn 180° at hub. Pull prey up with legs I and II. Manipulate with legs I and II, jaws and palps.

The hard and smooth exoskeleton of most coleopterans precludes rapid immobilization by biting. Small beetles, such as the weevils tested on *C. moluccensis*, would slip through the horizontal sheet unless immediately wrapped by the spider. Large *Melolontha* sp. were both active and heavy enough to break through the horizontal sheet, and escaped unless wrapped immediately. Beetles were also observed to slip through the ensnaring silk. This may explain the necessity for the long, repeated wrapping bouts given to *Melolontha* sp. Both weevils and scarabs were wrapped repeatedly at the hub during manipulation and early stages of feeding.

Beetles were never attacked by a simple wrap/bite sequence. The total handling time for melolonthiid beetles was significantly longer than for any other prey type. Perhaps penetration through a beetle's armour is difficult and a large number of short, exploratory bites are necessary before the spider can select a spot through which the venom and digestive enzymes can be injected. As a result, complete immobilization of the prey is slow and beetles must be wrapped repeatedly to avoid loss.

Both *Eriophora fuliginea* and *Argiope argentata* attacked *Tenebrio* beetles (about one-fourth the size of *Melolontha* sp.) with a repeated wrap/bite sequence, similar to that used by *C. moluccensis* on scarabs (Robinson and Olazarri 1971 Robinson et al. 1972). Robinson and Robinson (1973) tested *Melolontha* sp. on *Nephila maculata* and on *Argiope aemula* in New Guinea and found that although both responded with lengthy, complex sequences, *A. aemula* dealt more efficiently (more rapidly and with fewer losses) with the beetles than did the larger *N. maculata*. The latter lacks the wrap immobilization behavior, and attacks large prey by a repeated bite-and-back-off sequence. Thus, the wrapping attack, even when prolonged, is more effective with hard-cuticled prey such as beetles.

In 6 out of 13 complete predatory sequences, *Melolontha* were carried to the hub on silk. In the remaining instances, a distinct carry stage did not occur; rather, with each wrap/attach thread sequence, the prey was moved slightly closer to the hub. This method of transporting prey to the hub occurs frequently in several species of *Gasteracantha* and *Micrathena* (which do not carry prey on silk) with prey that are too heavy (or bulky?) to be carried in the jaws (Robinson and Lubin, unpublished). Probably carry-on-silk behavior evolved from this simpler but less efficient behavior sequence of wrap/attach thread to hub.

Sequences with Pentatomids.—Pentatomids (stink-bugs) were tested on *C. cylindroides*. Ninety percent were attacked by wrapping (sequence 2). The remaining 10% were given short test-bites (too short to measure accurately), and were then wrapped.

Pentatomids are well known to discharge noxious defense secretions (Eisner and Meinwald 1966). Twelve (60%) of the twenty pentatomids tested were actually observed to discharge a defensive secretion upon being attacked by the spider. Spiders that immobilize prey by wrapping (e.g., *Argiope* spp.) can attack pentatomids and other hemipterans with greater efficiency than can species with only bite immobilization behavior (e.g., *Nephila* spp.), as they can avoid the main force of the discharge (Robinson and Olazarri 1971). Similarly, bombardier beetles can escape more readily from spiders that attack by biting rather than wrapping (Eisner and Dean 1972).

In 60% of the sequences with pentatomids, spiders interrupted the attack, stopping to rest on or near the prey and clean the palps, legs and mouth parts. Spiders gave the appearance of being stunned by the discharge, remaining immobile for durations of a few seconds to over five minutes, before initiating cleaning or resuming the attack. Many attacks on pentatomids by *C. cylindroides* were unsuccessful. Nonetheless, remains of pentatomids and of other hemipterans were found in prey traps under *C. moluccensis* webs, indicating that this species, at least, does capture pentatomids under natural conditions (Lubin, unpublished).

Pentatomids, though lighter than blowflies, were always carried on silk. This is perhaps because of the noxious secretions. It is unclear how long it takes for the secretion to dissipate or become exhausted. Pentatomids were transported in the jaws by *A. argentata* (Robinson and Olazarri 1971), however, this may have been after a period of resting at the hub, having been left in the web for sufficient time for the secretion to disperse. In most instances, *C. moluccensis* did not begin to feed immediately after suspending a pentatomid at the hub, but remained resting at the hub or began cleaning. Thirteen out of 20 sequences with pentatomids were interrupted by resting or grooming behavior. Sequences with katydids of similar size were never interrupted. In 6 instances, interruptions in the capture sequence occurred just after the discharge of noxious secretion by the prey.

Table 6.—Comparison of attacks by *Cyrtophora*, *Argiope* and *Nephila* on similar prey types. Only predominant initial attack sequences are shown.

Prey	<i>Cyrtophora</i>	<i>Argiope</i>	<i>Nephila</i>
Moths	bite/wrap	long bite/wrap	bite
Blowflies, Houseflies	bite/wrap bite/pull out	wrap/short bite bite/pull out	seize and pull out
Orthopterans	wrap/bite wrap bite/wrap	wrap/short bite	bite and back off
Dragonflies	wrap/bite wrap bite/wrap	wrap/short bite	bite and back off
Beetles	wrap wrap/short bites	wrap/short bites	bite and back off
Pentatomids	wrap	wrap/short bite	—

Sequences with Multiple Prey.—Insects given to spiders that already had prey at the hub were treated in the same way as first prey. Second or third prey were not left in the web, but were carried back to the hub in a complete predatory sequence. This was determined by presenting multiple prey (fruitflies, blowflies, and katydids) to *C. citricola*, *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Many other species, including 7 *Argiope* species (Robinson 1975), *Arachnura* and *Gasteracantha* species (Robinson and Lubin, in press), leave second or third prey wrapped in the web, and return to feed on the first prey at the hub. Except in the case of very small fruitflies given to *C. citricola* in rapid succession, each successive insect is attacked and transported separately. All prey are suspended individually near the hub. The order in which they are eaten is not necessarily the same as that in which they were suspended. If the spider is already feeding on an insect at the hub, it will usually resume feeding on it after returning from another capture.

DISCUSSION

Similarities between predatory behavior units of *Cyrtophora* spp. and those of *Argiope* spp. and *E. fuliginea* have been noted throughout the text. Behaviors that did not occur in *Cyrtophora* but which occur in *Argiope* are maintenance of dragline connection with the hub (true of all araneids with sticky orbs), resting at the hub during a prey capture sequence, and “Rundgang” behavior (Peters 1931), involving multiple attachments of wrapped prey to the hub by dabbing the spinnerets against the hub as the spider turns in an arc of 180°. Web shaking is the only behavior observed in *Cyrtophora* that does not seem to have a functional counterpart in *Argiope* or *Eriophora*.

Attack sequences of *Cyrtophora*, *Argiope* and *Nephila* with similar prey types are compared in Table 6. *Cyrtophora* shares with *Argiope*, *Araneus*, *Eriophora* and *Arachnura* the ability to attack by wrapping and to free-wrap the prey by rotating the prey package while it is held away from the web. *Nephila*, *Herrenia*, *Micrathena* and perhaps *Gasteracantha* attack all prey by biting and do not rotate the prey while wrapping (Robinson 1975, Robinson and Lubin, in press; unpublished observations). The wrap/short bite sequence which *Argiope* uses with most prey other than moths is less

commonly used by *Cyrtophora*, and a broader spectrum of prey types may be immobilized by biting. Immobilization wrapping may have certain disadvantages for *Cyrtophora* due to peculiarities of the nonsticky knockdown web (see earlier).

It was suggested that environmental factors such as rain and wind, and prey availability in open habitats would select for the nonsticky web of *Cyrtophora* (Lubin 1973). The evolution of a new trapping method, along with drastic modification of web structure, appear to have modified the predatory behavior of *Cyrtophora* only slightly. I suggest that *Cyrtophora* is derived from an "advanced" araneid precursor in which complex predatory behavior including both wrapping and biting restraints already existed, and that only small changes in predatory behavior were necessary to comply with the new web type. These changes were:

1. Loss of a dragline connection with the hub during prey capture activities. As the *Cyrtophora* web is persistent, and accumulation of draglines on the horizontal orb might interfere with signal transmission to the hub and reduce the trapping efficiency of the spider. The dragline, considered a primitive form of silk production (Kaston 1964, Savory 1952), is probably found in all sticky-orb araneids, although few authors have remarked specifically on its presence. *Cyrtophora* species do not produce a dragline during locomotion under the sheet. The same is true for the related New World genus *Mecynogea* (personal observations) which constructs a *Cyrtophora*-type web. The dragline is used by many orb-weavers for rapid return to the hub, either by climbing up the thread (e.g. *Nephila*, in a "hand-over-hand" motion) or by swinging out onto a dragline beneath the plane of a horizontal web (e.g. *Leucauge*); for dropping out of the web when disturbed; and when hanging from the web surface during prey capture. In all these activities *Cyrtophora* dispenses with the use of a dragline. The lower barrier web would probably interfere with the spider swinging below the sheet on a dragline, and there is no advantage to walking on a dragline under a nonsticky sheet, over walking on the web itself. Furthermore, when disturbed *Cyrtophora* does not usually drop out of the web, but climbs into the barrier web or nearby vegetation. A similar escape behavior was observed in *Mecynogea lemniscata* (Exline 1948). During prey capture, *Cyrtophora* hangs from the web or from the prey by legs I and II (during wrapping) or by legs IV (during biting and feeding). As the sheet is uniformly strong and fine-meshed, it provides more even support to the spider moving under it than would a typical orb with its weak viscid spiral (in many instances, the viscid spiral alone could not support the weight of the orb weaver; see Lubin 1973). Based on these considerations, I would argue that the loss of dragline production in *Cyrtophora* during locomotion on the web came about with the evolution of the nonadhesive knockdown web.

2. Reduction in the use of wrapping for prey immobilization. Eberhard (1967) argued that immobilization by wrapping was an "advanced" trait, probably derived from post-immobilization wrapping at the capture site. Not all orb weavers share this trait (Robinson et al. 1969). Immobilization wrapping is an effective method of restraining large and/or dangerous insects. *Cyrtophora* does attack-wrap, but this method is reserved mainly for beetles, pentatomids, and hymenopterans (see also Blanke 1972), as well as some other large insects that can break through the horizontal sheet. As noted above, the sheet acts as a barrier

between the spider and its prey, making it safer to attack prey directly by biting and, at the same time, more difficult to restrain insects solely by wrapping.

3. *Cyrtophora* does not leave wrapped prey at the capture site. It shares this behavior with *Nephila*, *Herrenia*, *Gasteracantha* and *Micrathena*. Other araneids (e.g. *Argiope*, *Eriophora*, *Cyclosa*) often leave prey in the web after an immobilization- or post-immobilization wrap, particularly when a wrapped prey package is already present at the hub (Robinson 1975). There are two possible disadvantages to leaving prey in a *Cyrtophora*-type web. First, since *Cyrtophora* renews its web only infrequently (Lubin 1973), a dead insect in the sheet might be overlooked and thus lost or stolen by kleptoparasites. Second, in *Cyrtophora* wrapped insects hang below the sheet, attached by a single thread rather than rolled up along a radius and attached firmly at both ends, as is the case with prey left in sticky orbs. Prey packages left in *Cyrtophora* webs are probably more vulnerable to theft by kleptoparasites than prey left in sticky orbs.

4. *Cyrtophora* does not perform "Rundgang" behavior when hanging prey at the hub. As the function of this behavior is not known, it is difficult to speculate on reasons for its absence. Possibly this multiple attachment of prey to the hub serves to distribute prey weight evenly around the hub and/or to reinforce the hub. Since *Cyrtophora* has a horizontal sheet, there may be no need to distribute prey weight evenly around the hub; or *Cyrtophora* silk may be sufficiently strong so that multiple attachments to the hub are unnecessary. *Cyrtophora* webs have an open hub, but it is irregular in shape and the fine-meshed web around it lends strong, cross-braced support for suspended prey packages.

Kaston (1964) and Kullmann (1958, 1972, 1975: 373) suggested *Cyrtophora* as a link between the sheet web-building Linyphiidae and the Araneidae. Earlier, McCook (1889) suggested that the related New World genus *Mecynogea* (the "Basilica" spider) was similar to the Linyphiidae in its manner of web construction. Kaston (1964) placed *Cyrtophora* and *Mecynogea* between the linyphiids and the genus *Nephila* in his scheme of the evolution of spider webs, based on the following similarities: (1) *Cyrtophora* and some linyphiids construct a non-adhesive, 3-dimensional, knockdown web; (2) both *Cyrtophora* and *Nephila* have irregular barrier webs on either side of the orb; (3) *Cyrtophora* and *Nephila* webs have bifurcated radii toward the periphery of the orb and retain the non-adhesive, structural spiral (*Nephila* webs have a viscid spiral as well).

The linyphiid web consists of an irregular-mesh, horizontal sheet with a barrier web above and below it. The sheet, which may be domed or tent-shaped (as in the web of *Linyphia marginata*), lacks the basic elements of an orb web: radii, spiral and hub. It is difficult to imagine the complex web of *Cyrtophora* derived from the unstructured sheet-web of a linyphiid. Structural similarities between *Cyrtophora* webs and those of linyphiids are probably superficial ones, resulting from convergent evolution. Blanke too (1972) regarded the similarities between *C. citricola* and the linyphiids as convergent evolution and noted that, in all aspects of morphology and behavior, *C. citricola* was an araneid. Exline (1948) arrived at the same conclusion regarding *Mecynogea*, based both on web structure and on spider morphology.

The implied relationship between *Cyrtophora* and *Nephila* is equally tenuous. The barrier web of *Nephila* is derived from a rudimentary orb web (Robinson and Robinson 1973), while there is no evidence that this is the case in *Cyrtophora*. Forked radii occur in webs of several araneids, including *Eriophora fuliginea*, and are therefore not unique to *Cyrtophora* and *Nephila*. They may be characteristic of large orb webs where constant

mesh size is desirable. Without forked radii, mesh size would increase markedly toward the periphery of a large orb. Egg sacs of *Cyrtophora* are more similar to those of *Argiope* than of *Nephila* (Kullmann 1961; unpublished observations). The courtship behavior of *C. citricola* (Blanke 1972) and of *C. nympha* in Panama (Robinson and Robinson, in press) is of an "advanced" type, most similar to that of certain *Araneus* species. Levi (1978) noted that, based on morphological similarities, both *Cyrtophora* and *Mecynogea* are "related, but not closely, to *Araneus*" (p. 741). Finally, based on predatory behavior, I contend that *Cyrtophora* is quite removed from both the linyphiids and the nephilids. *Cyrtophora* predatory behavior is similar to that of *Argiope*, *Araneus*, and *Eriophora*, and includes the advanced behaviors of immobilization wrapping, throwing bands of silk onto the prey from a distance, and rotating the prey during the post-immobilization wrap. Prey immobilization by wrapping does not occur in linyphiids (Bristowe 1941, Eberhard 1967) or in *Nephila* (Robinson et al. 1969, Robinson and Mirick 1971). On this evidence alone, it seems unlikely that *Cyrtophora* separated from the main line of araneid evolution prior to the separation of the Nephilinae from the rest of the araneid line. The differences between the predatory behaviors of *Cyrtophora* and *Argiope* are relatively minor and may represent changes in behavior associated with the evolution of a specialized web.

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THE EYED SCHIZOMIDS, WITH A DESCRIPTION OF A NEW SPECIES FROM SUMATRA (SCHIZOMIDA: SCHIZOMIDAE)

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ABSTRACT

A review of the eyed schizomids is presented: *Trithyreus cambridgei* Thorell is considered a *species inquirenda*; *Schizomus bagnallii* (Jackson) is redescribed; and *Schizomus biocellatus*, new species, is described.

INTRODUCTION

At present the controversy concerning the two genera of the subfamily Schizominae, *Trithyreus* and *Schizomus*, cannot be resolved. In the past the presence or absence of a split metapeltidium was used to separate the two genera. Many observers (Hansen and Sørensen 1905, Lawrence 1969, Rowland 1973, Rowland and Reddell 1979) have expressed doubts about the value of this character at the generic level, citing variation (both interspecific and intraspecific) as reason for their doubts. Rowland and Reddell (1979) stated that the genus *Trithyreus* should be restricted to contain only the type species, *T. grassii* Thorell, and that all other members formerly included in that genus should be placed in the genus *Schizomus*. I will follow this suggestion in this paper.

Schizomids typically lack eyes, or have only weak eyespots on the anterolateral portion of the carapace, but there have been two previous descriptions of schizomids having "true" convex ocelli. Thorell (1889) described *Trithyreus cambridgei* Thorell from the only known specimen, an immature. This specimen, now mutilated to where comparisons are impossible (Hansen and Sørensen 1905), is presumably lost (J. Reddell, personal communication), so *T. cambridgei* must be considered a *species inquirenda* at this time. The second species, *Schizomus bagnallii* (Jackson), presents an interesting problem itself, because its true geographical distribution is unknown. It was collected in 1907 in the Kew Botanical Gardens of London, England, and is doubtlessly an import. However, it will be redescribed here, based on more useful characters than were used in the original descriptions (Jackson 1911a, 1911b). The major contribution of this paper will be to describe a third species of eyed schizomid collected near Bukittingi, Sumatra in 1925.

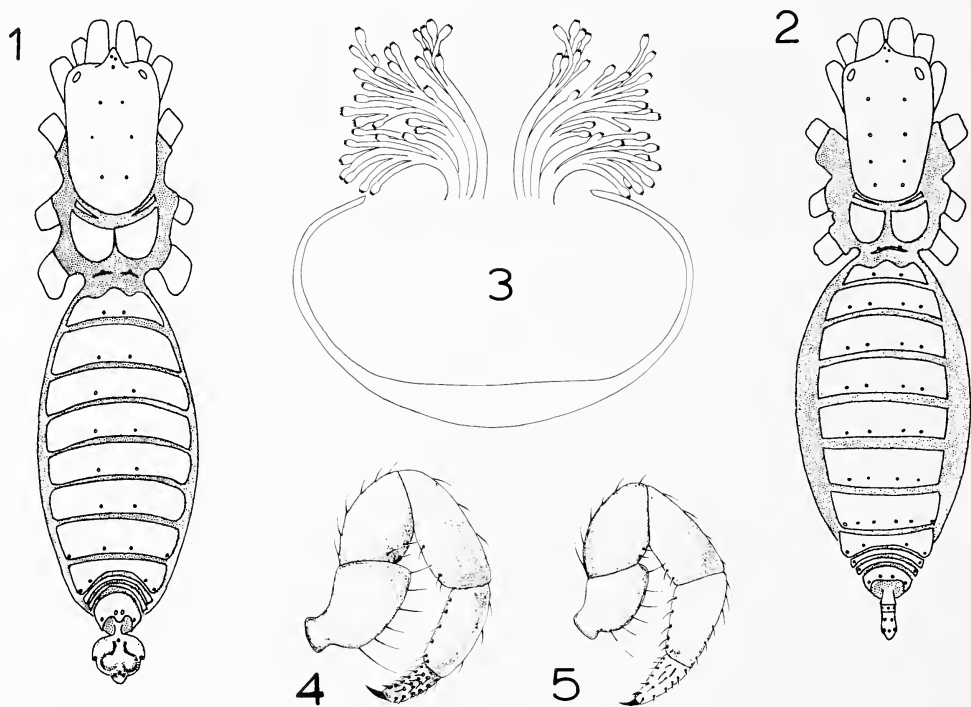
Schizomus biocellatus, new species

Figs. 1, 3, 4, 6-10

Type data.—All types were collected in 1925 in Fort de Kock (now Bukittingi), Sumatra, elev. 920 m., by E. Jacobson. They are deposited as follows: Holotype male, 162 paratype males, 498 paratype females and immatures, NHM, Wien; two paratype males, one paratype female, and one paratype immature, BM; two paratype males, one paratype female, and one paratype immature, AMNH.

Distribution.—Known only from the type locality.

Diagnosis.—Based on adults only. Total length of male (from tip of first cheliceral segment to tip of flagellum; five specimens, range with mean in parentheses) 3.55-3.80 (3.68) mm, of female 3.50-4.35 (3.96) mm; carapace with convex vitreous ocelli, three apical setae, three pair dorsal setae; metapeltidium divided; flagellum of male strongly convex with two dorsolateral elevations, flagellum of female three-segmented; pedipalps of male variable in length; female spermathecae consisting of four pairs of multibranched stalks terminating in sclerotized bulbs.



Figs. 1-5.—1, dorsal view of male paratype *Schizomus biocellatus*, new species, illustrating only coxae of pedipalps and legs and setal pits of carapace and abdominal terga; 2, dorsal view of female lectotype *Schizomus bagnallii* (Jackson), illustrating same structures as Fig. 1; 3, spermathecae of *S. biocellatus*; 4, right pedipalp of female paratype *S. biocellatus*; 5, right pedipalp of female lectotype *S. bagnallii*.

Table 1.—Measurements (mm) of leg segments of five adult males and five adult females of *Schizomus biocellatus*, new species. For convenience, the measurement of the pedipalp Tarsus-basitarsus is listed by Basitarsus.

		Pedipalp	Leg I	Leg II	Leg III	Leg IV
Trochanter	♂	0.50–0.85	0.30–0.40	0.20	0.15–0.20	0.25–0.30
	♀	0.35–0.40	0.25–0.30	0.15–0.20	0.15	0.25
Femur	♂	0.80–2.30	1.15–1.25	0.70–0.85	0.65–0.80	1.10–1.20
	♀	0.35–0.40	1.00–1.05	0.70–0.75	0.55–0.65	0.95–1.10
Patella	♂	0.85–2.25	1.30–1.50	0.35–0.45	0.25–0.30	0.40–0.45
	♀	0.45	1.15–1.25	0.35–0.40	0.25–0.30	0.35–0.45
Tibia	♂	0.45–0.70	0.80–1.05	0.40–0.50	0.30–0.35	0.70–0.80
	♀	0.35–0.40	0.70–0.85	0.40–0.45	0.30–0.35	0.65–0.70
Basitarsus	♂	0.20–0.25	0.30–0.40	0.45–0.55	0.45–0.55	0.65–0.70
	♀	0.20	0.30–0.35	0.40–0.45	0.40–0.50	0.60–0.65
Tarsus	♂		0.45	0.35–0.40	0.35–0.40	0.40–0.45
	♀		0.35–0.45	0.30–0.40	0.30–0.35	0.35–0.45

Description.—Male (Fig. 1). Cephalothorax: Carapace length 1.04-1.40 (1.06) mm, strongly convex, twice as long as wide, terminating anteromedially into sharp conical process; ocelli distinct, vitreous cornea more convex than adjacent carapace; three apical setae, three pair dorsal setae; mesopeltidia very narrow, pointing medially; metapeltidium divided medially into two plates, anterior margin of each parallel to mesopeltidia and posterior margins rounded; anterior sternum subtriangular, pointing caudally, with 11 setae; posterior sternum subtriangular, with eight setae. Abdomen: Abdominal tergum I very narrow, equidistant between metapeltidia and abdominal tergum II, with two setae; terga II-VII with two dorsal setae; tergum VIII with two dorsal and two lateral setae; tergum IX with two dorsolateral and two lateral setae; segment X with 10 setae; segment XI with seven setae; segment XII with 10 setae. Flagellum (Figs. 8-10): Length 0.30-0.40 mm, dorsal surface strongly convex, having two dorsolateral elevations, terminating in small cone, 16 major setae. Pedipalps (Figs. 6, 7): Length highly variable, with elongation of trochanter, femur, and patella; or like female; single subapical spur located ventrally on tarsus-basitarsus; claw not quite one-third as long as upper margin of tarsus-basitarsus; for measurements, see Table I. Legs: Leg I antenniform; coxa of leg II with anterolateral spur; femur of leg IV little more than half as long as wide; legs II-IV with three tarsal claws.

Females. Like males with the following exceptions. Abdomen: terga VI-VII with four setae. Flagellum: Length 0.25-0.30 mm, consisting of three segments, second segment much shorter than first, third longer than first and second combined; first segment, no setae; second, four; third, twelve. Pedipalps (Fig. 4): Little more than half as long as body; trochanter, femur, patella not elongate. Spermathecae (Fig. 3): Consisting of four pairs of multibranched stalks, each branch terminating in sclerotized bulbs.

Variation.—*Schizomus biocellatus* exhibits intrasexual variation in the length of the pedipalps of the males. There may be elongation of the trochanter, femur and patella, or the pedipalps may be short as in females. Approximately 75% of the males in the type series have elongated pedipalps, with the remainder having short or intermediate pedipalps. Females differ from males in the number of setae on abdominal terga VI and VII, as well as in pedipalp length.

Comparisons.—*Schizomus biocellatus* differs from all other schizomids, excluding *Trithyreus cambridgei* Thorell and *Schizomus bagnallii* (Jackson), in that it possesses

convex vitreous ocelli. It cannot be compared to *T. cambridgei*, *species inquirenda*, for reasons stated earlier, and inadequate descriptions of the type. *S. biocellatus* differs from *S. bagnallii* in the setational pattern of the carapace and abdominal terga.

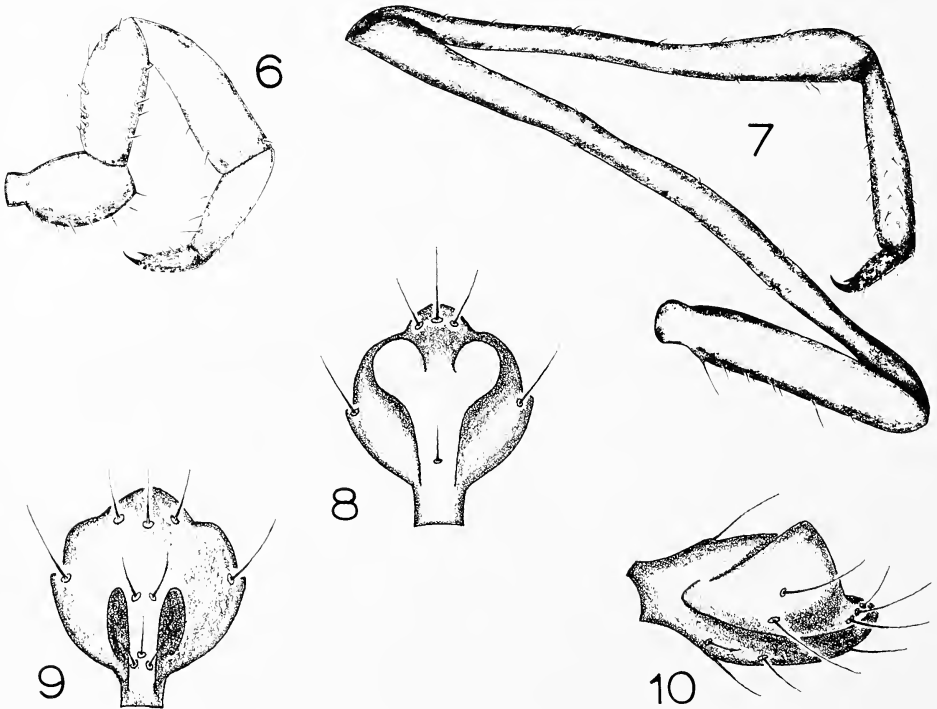
Schizomus bagnallii (Jackson), new combination
Figs. 2, 5

Trithyreus bagnallii Jackson 1911a: 75, 1911b: 438, figs. 1-5.

Type data.—From the original type series, I designate a lectotype female collected in the Kew Botanical Gardens in London, England by R. S. Bagnall during the 1907 Kew Gardens Survey, deposited BM; also, a paralectotype female and two paralectotype immatures from the same locality, same date, and same collector, BM.

Distribution.—Known only from four specimens collected at the Kew Botanical Gardens in London, England; doubtless imported.

Diagnosis.—Based only on adult females (males unknown). Total length (from tip of first cheliceral segment to tip of flagellum) 3.50-3.55 mm; convex vitreous ocelli present on carapace; three apical setae, four pair dorsal setae; metapeltidium divided; flagellum consisting of three segments.



Figs. 6-10.—External anatomy of *Schizomus biocellatus*, new species: 6 and 7, right pedipalps of males showing variation in length; 8, dorsal view of male flagellum; 9, ventral view of male flagellum; 10, lateral view of male flagellum.

Table 2.—Measurements (mm) of leg segments of lectotype female and paralectotype female of *Schizomus bagnallii* (Jackson). For convenience, the measurement of the pedipalp Tarsus-basitarsus is listed by Basitarsus.

	Pedipalp	Leg I	Leg II	Leg III	Leg IV
Trochanter	0.20–0.25	0.25–0.30	0.15	0.15	0.20
Femur	0.30–0.35	0.80	0.60–0.65	0.50	0.85–0.90
Patella	0.35	0.75–0.95	0.25–0.30	0.20–0.25	0.30–0.35
Tibia	0.30	0.60–0.65	0.30–0.35	0.25–0.30	0.55–0.60
Basitarsus	0.20	0.25–0.30	0.30–0.40	0.30–0.35	0.50
Tarsus		0.35	0.25–0.30	0.30	0.40

Description.—Based only on females (Fig. 2). Cephalothorax: Carapace length 0.85-0.95 mm, strongly convex, not quite twice as long as wide, terminating anteromedially into sharp conical process, ocelli distinct, vitreous cornea more convex than adjacent carapace, three apical setae and four pair dorsal setae; mesopeltidia very narrow, acutely triangular and pointing medially; metapeltidium divided medially into two plates, anterior margin of each parallel to mesopeltidia, posterior margins rounded; anterior sternum subtriangular, pointing caudally, possessing 11 setae; posterior sternum subtriangular, possessing eight setae. Abdomen: Abdominal tergum I very narrow, equidistant between metapeltidia and abdominal tergum II, possessing two setae; tergum II with two setae; terga III-VII with two dorsal and two lateral setae; tergum VIII with two dorsal, two dorsolateral, and two lateral setae; tergum IX with two dorsolateral, two lateral setae; tergum X with nine setae; segment XI with seven setae; segment XII with fourteen setae. Flagellum: Length 0.25 mm, consisting of three segments, second segment much shorter than first, third longer than first and second combined; first segment, no setae; second, four; third, 12. Pedipalps (Fig. 5): Trochanter produced distally; single subapical spur located ventrally on tarsus-basitarsus; claw not quite half as long as upper margin of tarsus-basitarsus; for measurements, see Table 2. Legs: Leg I antenniform; coxa of leg II with anterolateral spur; femur of leg IV more than twice as long as wide; legs II-IV with three tarsal claws. Spermathecae: Not dissected.

Variation.—No variation, other than size, was noted.

Comparisons.—See under *S. biocellatus*.

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VIBRATION IN *HETEROPODA VENATORIA* (SPARASSIDAE): A THIRD METHOD OF SOUND PRODUCTION IN SPIDERS¹

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ABSTRACT

Pheromone-stimulated male *Heteropoda venatoria* (L.) produce sounds during bouts of leg oscillations while coupled to the substratum by their tarsal adhesive hairs. No stridulatory organ is involved. Preventing palpal percussion and abdominal vibration does not eliminate primary sound production. Leg oscillation rates of 63, 83, and 125 Hz, roughly estimated from high-speed cinematographic samples of signalling, were within 1 SD of the mean frequencies of the lowest ($\bar{Y} = 88$ Hz) or highest ($\bar{Y} = 146$ Hz) frequency wave-trains, as indicated by oscillographic analysis of such sounds. These signals resemble and are analogous in origin to insect flight-sounds, the fundamental frequency being determined directly by the appendage oscillation rate. Hypotheses about the roles of vibration in these and other spiders, including araneids, are considered.

INTRODUCTION

Sound production in spiders usually involves stridulatory organs or, less frequently, percussion (Legendre 1963; Rovner 1975). We now can add to stridulation and percussion a third method of sound production, one which is analogous to the generation of flight-sounds in insects. During pre-copulatory bouts of vibration males of the nocturnal, long-legged, wandering spider *Heteropoda venatoria* (L.) produce a sound faintly audible to the unaided human ear as a low-frequency "buzz" or "hum".

METHODS

In late June, 1978, I collected penultimate and adult *H. venatoria* at night in an avocado (*Persea americana*) orchard at the University of Florida's Agricultural Research and Education Center in Homestead, Florida. After being transported to my laboratory in Ohio, the spiders were maintained in their individual cages with a constant water supply and weekly feedings of crickets (*Acheta domesticus*) and, occasionally, large dipterans.

¹ This study was supported by NSF grant BNS 76-15009.

All the immature spiders reached adulthood by mid-July. Adult males had a body length of 17 mm. I observed reproductive behavior in the late evening (usually between 2100 and 2300 hr) during July-October. Temperatures ranged from 17 to 22°C.

For each recording or filming session, I introduced one of three males to a vacant glass cage (terrarium or battery jar) that had just been occupied by a female conspecific. To record the air-borne components of the signal, I used a PML condenser microphone (Model DC-21) suspended about 5 cm above a horizontal substratum of dead avocado leaves. (When collected, most of the spiders were observed resting on such dried leaves beneath the trees or on the living leaves of the lower branches of the trees.) To record the substratum-borne component of the sound, I attached a high-sensitivity vibration pickup (General Radio, Type 1560-P14) to a vertical cardboard substratum. Oscillograms were obtained with a Tektronix oscilloscope (Model D44) and a Grass kymograph camera (Model C4) running at 100 or 25 mm/sec. Sonographic analyses involved use of a Voice Identification Inc. sound spectrograph (Series 700). Portions of courtship were filmed with a Cine-8 Super 8mm camera (Visual Instrumentation, Model SP-1) at 250 frames/sec.

To determine experimentally whether palpal contact with the substratum is essential for sound production, as usually is true in another family of wanderers, the lycosid spiders, I placed both palps of one male in a paraffin-fixed, human hair sling above the anterior cephalothorax (see Rovner and Wright 1975 for technique). To prevent abdominal oscillations, I attached the abdomen of this same male to the cephalothorax with a paraffin bridge. Both operations involved CO₂ anesthesia. In this paper, means are accompanied by S.D.'s.

RESULTS

Courtship Behavior.—After introduction to the female's vacated cage, the male wandered over the walls, ceiling, and floor. He alternated bouts of palpal exploratory behavior with longer periods in which he was stationary. At the latter times, the tarsi of all of the widely spread legs were fixed to the vertical or horizontal substratum and the body partly elevated (Fig. 1). While in this rigid position, the male performed bouts of vibration, during parts of which, buzzing or humming sounds could be heard by the unaided ear up to at least 0.3 m away, even when the spider was on glass. Downward jerks of the body, each accompanied by a single caudal palpal scrape, occurred at intervals. Very brief, broad-spectrum noises sometimes were coincident with these body jerks.

Oscillographic Analyses.—Sound production resulting from appendage oscillations involved a series of intermittent, very low amplitude "minor" wave-trains that culminated in a louder primary signal lasting approx. 2.5-4.0 sec (Figs. 2 and 3). The primary signal usually contained four distinct wave-trains. It began with several (3.8 ± 2.62 , $n = 25$) closely spaced, brief wave-trains that I termed "pre-majors," which usually showed successive increases in amplitude. These typically were followed by a longer, two-part wave-train, "major, A and B", that had higher frequencies and relatively homogeneous waves. High-amplitude waves were characteristic of the major A wave-train, while those of the major B could be of either lower or higher amplitude than the major A. (During bouts of low intensity courtship, the major A and B wave-trains were not as distinctive as those in Figs. 2 and 3.) The final portion of the primary signal was of lower amplitude than the

major but contained the highest frequencies in its several wave-trains called "post-majors". Thus, the primary signal of untreated males showed a trend of increasing frequencies in successive wave-trains (Table 1). This increase in pitch as each primary signal progressed toward its end point was readily audible to the human ear.

Two-tailed *t*-tests were used here and later to test the hypothesis that there was no difference between the mean frequencies of each type of wave-train for those samples having similar variances. In the case of the untreated males, the post-major wave-train had a higher frequency than the pre-major ($t = 10.63, P < 0.001$). Likewise, the major B wave-train had a higher frequency than the preceding major A wave-train ($t = 6.87, P < 0.001$).

After the primary signal ended, an inactive period or a bout of exploratory behavior often occurred during a relatively quiet period lasting 36.7 ± 19.60 sec ($n = 30$). Then there was a series of very low amplitude minor wave-trains during a variable interval lasting 28.8 ± 21.74 sec ($n = 28$), this series giving way to another primary signal. Thus, the pattern of courtship signalling in male *H. venatoria* is an alternation of a relatively quiet period that includes low-level sound-bursts with a period consisting of the louder primary signal.

As shown in the sample oscillograms (Figs. 2 and 3), most of the acoustic signal consists of relatively simple, often sinusoidal-like waveforms. This suggests that little energy is present as harmonics above the fundamental frequencies. The sonographic analyses supported this interpretation, harmonics of the vibration-generated fundamental frequency being present only in certain parts of the signal and not extending above about 800 Hz.

Signalling by the Treated Male.—Neither preventing palpal contact with the substratum nor preventing abdominal oscillations resulted in a loss of sound production in the male so treated. There was no difference between this male and the untreated ones as to the frequencies of the pre-major ($t = 0.85$, NS) or post-major ($t = 1.40$, NS) wave-trains.

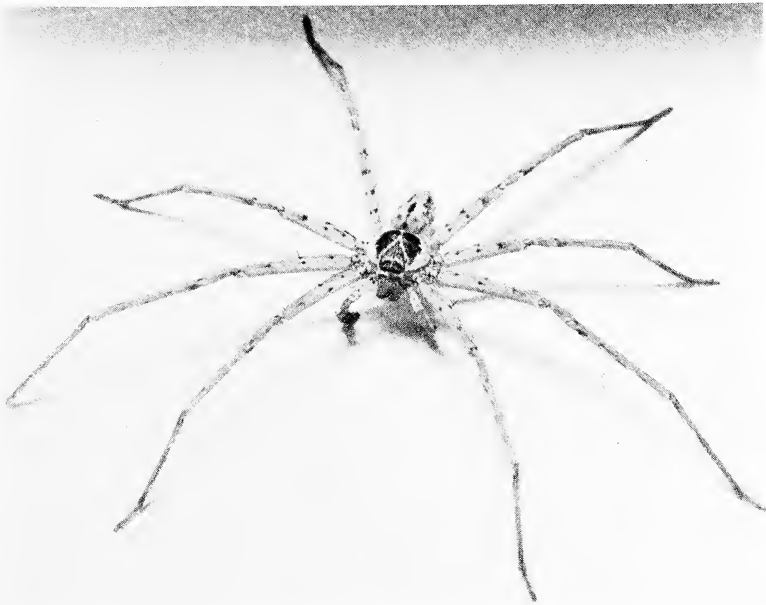


Fig. 1.—*Heteropoda venatoria* in the courtship posture on the wall of a cage (approx. 1.4 X). The camera was aimed obliquely upward.

Within the signal of the treated male, the typical increase in frequency between the pre- and post-major wave-trains occurred ($t = 4.56, P < 0.001$). However, the major wave-train frequencies of the treated male were lower than in the untreated males (major A: $t = 6.75, P < 0.001$; major B: $t = 6.36, P < 0.001$) and the form of the signal was altered (Fig. 3). In another experiment a male lacking legs I produced sounds like those of intact males.

Cinematographic Analyses.—Slow-motion and frame-by-frame analyses of filmed samples of behavior in courting male *H. venatoria* revealed low-amplitude, vertical oscillations of the posterior pairs of legs and the abdomen. At times, leg oscillations involved only legs IV. Two, three, or four frames of film were required for completion of each oscillation, depending on the portion of courtship or the intensity of courtship being sampled. Thus, some sections of the films contained a series of 2-frame oscillations; others, 3-frame; yet others, 4-frame. At a camera speed of 250 frames/sec., these represent vibration rates of roughly 125, 83, and 63 Hz respectively. The highest rate of oscillation, 125 Hz, occurred in legs IV. These filmed oscillation rates fell within 1 SD of the mean frequencies of either the lowest or the highest frequency wave-trains obtained in the oscillograms of the primary signals (Table 1).

Slow-motion analyses also revealed that the body jerks occurring at intervals during courtship involved ventro-caudad dips of the body during which the palps were swept caudad from their otherwise stationary position. The body movements were derived from sudden changes in the degree of flexure of the proximal joints of the legs, especially the posterior pairs. Dips were 0.04 sec in duration. The interval from the onset of one dip to the onset of the next averaged 0.15 ± 0.03 sec ($n = 15$). This was similar to the interval between onsets of minor wave-trains (0.20 ± 0.07 sec; $n = 22$) in one of the oscillograms. An additional behavior revealed in one male that was filmed was a rapid waving of legs II during part of the intense vibration that occurs during primary signal production.

DISCUSSION

Mechanism of Sound Production.—Although courting male *H. venatoria* produce occasional noises percussively when body jerks occur, most of their acoustic signal is generated without the mechanisms known to function in other spiders—stridulation and percussion. The similarity of values for leg oscillation rates (determined cinematographically from samples of this behavior) and the fundamental frequencies of the primary signals (determined oscillographically from other samples of this behavior) suggests that *H. venatoria* produces humming sounds the same way that many winged



Fig. 2.—Oscillogram illustrating the wave-train components of the primary signal of courting male *Heteropoda venatoria*. Several "pre-major" wave-trains give way to a two-part "major" wave-train, which is followed by several "post-major" wave-trains containing the highest frequency sounds.

insects do, by the tuning fork-like effect of appendage vibrations that set up regions of compression and rarefaction (Haskell 1961).

The films suggest that vibration of the posterior legs, especially legs IV, are of major importance in generating the primary signal. Neither the palps nor the abdomen play a role in producing the fundamental frequency of this sound. Indeed, the abdominal vibrations during sound production in this species may be a purely passive, induced movement—a by-product of the leg oscillations.

Vibration in Other Arthropods.—*H. venatoria* has wave-trains that are within the range of the flight-sounds of certain coleopterans (75-100 Hz) and, in its upper range of pitches, overlaps the flight-sounds of some familiar hymenopterans (*Bombus* sp., 150 Hz) and dipterans (*Musca domestica*, 150-200 Hz) (Sotavalta 1963). Even when not flying, sound generation by appendage vibration occurs in insects: “piping” by holding the wings and thorax in a state of fine tremor in queen honeybees (*Apis mellifera*), and “singing” by vibrating only the wing bases in syrphid flies resting between flights (ibid.). The low, humming sound produced by vibration of the flexed large cheliped in male fiddler crabs (*Uca pugilator*) provides an example of this type of sound production in yet another class of arthropods (Burkenroad 1947). Although common in flying insects, such sound production by appendage vibration is otherwise rare in this phylum (Dumortier 1963), *H. venatoria* now being added to the few wingless arthropods using this mode.

Factors Affecting the Sounds.—As in the insects and crustaceans, resonance of the spider's body or appendages, friction at joints, or other factors sometimes add harmonics to the fundamental frequency, thereby producing the more complex wave-forms that

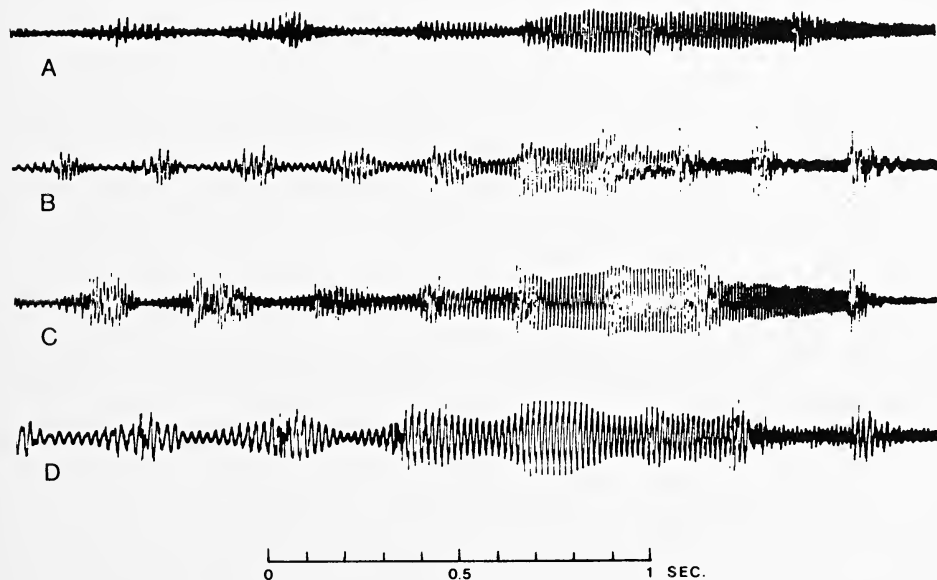


Fig. 3.—Oscillograms of primary signals of courting male *Heteropoda venatoria* arranged with the onsets of the major wave-trains lined up vertically (just to the right of center). (A) Airborne sound transduced by a condenser microphone; substratum of dried leaves. (B-D) Solid-borne sounds transduced by a vibration pickup; cardboard substratum. A, B and C were recorded from untreated males, while D was from a male with its palps in a paraffin-fixed sling and its abdomen attached with paraffin to its cephalothorax.

Table 1.—Mean frequencies (Hz) of wave-trains in courting male *Heteropoda venatoria*. (See Fig. 2).

	Pre-major	Major A	Major B	Post-major
Untreated Spiders	87.5 ± 24.76 (n=40)	93.7 ± 5.16 (n=15)	108.3 ± 6.45 (n=15)	145.7 ± 19.46 (n=30)
Treated Spider	81.0 ± 26.40 (n=15)	71.3 ± 8.54 (n=4)	83.8 ± 8.54 (n=4)	134.0 ± 31.43 (n=10)

occur at various points in the signal. In another regard, adding paraffin to parts of the body surface (and attaching major body parts to each other) changes the dynamics of the oscillatory movement. It has an effect similar to that caused by loading insect wings with collodion, which lowers the wingbeat frequency (Sotavalta 1963). This probably accounts for the reduced fundamental frequencies of the wave-trains produced by the male *H. venatoria* that was treated to prevent palpal percussion and abdominal vibration.

Importance of Substratum Coupling.—The attachment of *H. venatoria* to the substratum by the well-developed adhesive hairs of the claw tufts (Homann, 1957) is important in the effectiveness of this species' method of acoustic communication. The tetanic-like oscillations appear to involve considerable force. Were the posterior leg tarsi to slip on the substratum, the output of the mechanism generating the primary signal would be diminished. Furthermore, due to the spider's high sensitivity to solid-borne vibrations, it is likely that the substratum is the best medium for signal transmission. Playback experiments in lycosids indicated that substratum-conducted courtship sounds yielded stronger, more oriented responses from females than did airborne (Rovner 1967). Data obtained in the present study encourage me to put forth a generalization that sound production by wandering spiders always includes a substratum component, whether the mechanism be stridulation or percussion in lycosids (Rovner 1975; van Helsdingen personal communication), percussion in *Anyphaena accentuata* (Bristowe 1958), or vibration in *H. venatoria*.

Role of the Airborne Component.—Coupling to the substratum increases the loudness of the airborne acoustic component by incorporating the substratum into the system as a sounding-board. Based on the ability of lycosids to respond to airborne courtship sounds (Rovner 1967) and on the ability of *H. venatoria* to detect and capture insects that fly nearby (Rovner, unpublished data), it is likely that female *H. venatoria* receive the male's airborne sound by the single slit sensilla of the tarsi (Barth 1967), as well as use the trichobothria to detect air movements produced by the male's vibration (Görner and Andrews 1969). It probably is more than a coincidence that the male's signal involves frequencies like those of flying insects that are included in this species' diet. In spiders, the resolution and tuning of the primary sensory equipment for prey detection usually are adapted also for intra-specific communication.

Vibration in Other Sparassids.—The occurrence of acoustic signalling in *H. venatoria* suggests that future studies will reveal other sparassids to be using this mode of communication. Indeed, males of the Australian huntsman spider, *Isopoda immanis*, were described as having "violent tremors" of the body as well as shaking and drumming of the palps during various stages of courtship, although there was no mention of audible sounds (Coleman in McKeown 1952). A large wandering spider whose humming sound is regarded as a sign of good luck when heard in African huts may turn out to be another

sparassid, but perhaps is the widely distributed *H. venatoria* itself (Brady, personal communication).

Vibration in Other Wandering Spiders.—The finding of sound production in a spider that does not use stridulation or percussion to generate its primary signal raises the possibility that some portion of the total sound output of spiders that do use such methods also may be produced by the coincident vibrations of the abdomen or appendages. Such sounds normally would be masked by the louder output of the stridulatory organ or the percussive action. Evidence for this being so was obtained in male *Lycosa rabida* whose palps were fixed to the cephalothorax to prevent palpal stridulation and percussion. A faint whirring sound was detectible when such males were monitored by a vibration pickup, even after the abdomen was attached to the cephalothorax to prevent abdominal oscillations (Rovner 1975). In other words, when one shuts off the primary sound generator, lower-amplitude sounds resulting from appendage oscillations are detectible.

Vibration in Web-weaving Spiders.—In closing, I should like to speculate about the rapid, high-amplitude oscillations seen in certain web-weavers such as araneids when they are disturbed. This behavior ("web flexing") results in the spider becoming blurred; thus, it is hypothesized that the function is to reduce the visual target available to predators or to make onset of contact difficult (Tolbert 1975). In light of the data obtained in the present study, is it possible that such oscillations also mimic the wing-beat frequencies of certain hymenopterans as a means of driving away hymenopteran or other predators? The presence of silk stabilimenta placed radially with respect to the spider would improve the wing-beat mimicry produced by the oscillations, offering yet another hypothesized function for these web structures. To be effective, such a mechanism need not generate sounds audible to our ears but merely displacement waves detectible by arthropods at close range. In other words, is the spider scaring the predator as well as being elusive?

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ERRATUM

The Editor regrets the following error which may cause considerable confusion: on vol. 7, no. 3, pp. 176 and 178 are transposed and misnumbered. The description of *Eustiromastix major* Simon, 1902, starts on p. 174 and continues on p. 178; that of *E. keyserlingi* (Taczanowski, 1879), starts on p. 178 and continues on p. 176; finally, that of *E. vincenti* (Peckham y Peckham, 1893), starts on p. 176 and continues on p. 179.

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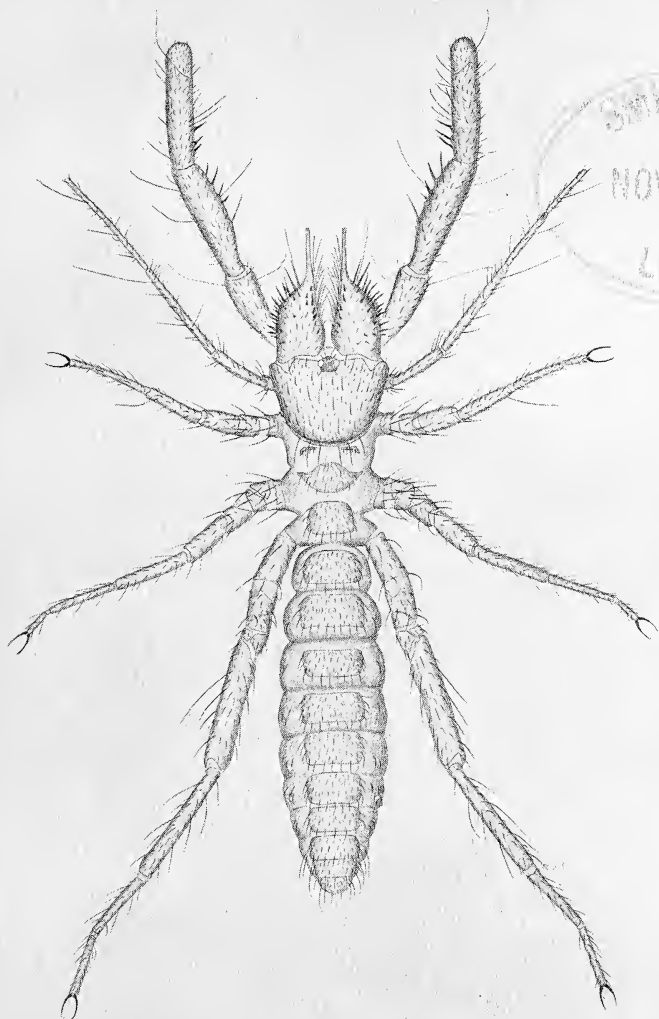
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MORPHOLOGICAL AND ETHOLOGICAL ADAPTATIONS FOR PREY CAPTURE IN WOLF SPIDERS (ARANEAE, LYCOSIDAE)¹

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ABSTRACT

High-speed cinematography and experimental modification of morphological features were used to study the adaptations of lycosid spiders for capturing large, dangerous prey. Removal of the scopula hairs from the legs (by shaving) reduced the spider's ability to restrain crickets from escape. Observations suggested the importance for prey capture of other features of the legs: (1) a primarily flexor musculature for grasping strength; (2) an efficient hydraulic mechanism for rapid extension; (3) erectile spines for protection from the prey; and (4) relatively great length, permitting manipulation of prey at a safe distance from the body. Captures involving "de-fanged" spiders indicated that the chelicerae alone are sufficient for prey retention, neither fangs nor legs being needed during cheliceral grasping. Captures involving spiders prevented from using their chelicerae and fangs suggested that the venom apparatus is essential only for immobilization of already-restrained large prey so that ingestion can begin. Descriptive data point to prey capture being a family-specific behavior; consequently, there has evolved a diversity of guilds within the wandering spiders.

INTRODUCTION

The ability of wandering spiders to overpower relatively large prey involves several heretofore little-studied structural and behavioral adaptations. Some specializations make up for the lack of a silk trap, which aids web-weavers by interrupting the prey's locomotion and by restraining it from escape during subsequent handling. Another specialization, the venom apparatus, is present in all wandering spiders and most web-weaving spiders; however, its role has not been examined with regard to its relative importance in the overall predatory sequence. The present study includes the first experimental investigation of the roles of these various morphological adaptations in prey capture by wandering spiders.

¹This study was supported by National Science Foundation Grant BNS 76-15009.

By means of high-speed cinematography, I was able to examine the predatory behavior of several species of *Lycosa*. Much of this behavior resembled that of the ctenid *Cupiennius salei* (Keyserling) studied by Melchers (1967). Based on Melchers' and my data, I developed hypotheses about the functions of various appendage adaptations; then I observed the behavior of experimentally modified spiders to test these hypotheses. Significant roles were indicated for the adhesive scopula hairs and the erectile spines on the legs. In addition, support was provided for Anderson and Prestwich's (1975) hypothesis that the preponderance of flexor muscles in the legs of spiders improves prey-holding ability, and Enders' (1975) hypothesis that the venom apparatus evolved in spiders to enable them to utilize large prey and thereby obtain more food per capture than would a non-venomous predator of similar size. Finally, the concept of a "guild of wandering spiders" was questioned in light of ideas generated in the present study, as was Enders' (1975) hypothesis that webs evolved in spiders as tools for subduing larger prey than nonweb spiders can handle.

METHODS

Most observations were made on adult female *Lycosa rabida* Walckenaer, *L. aspersa* Hentz, and *L. helluo* Walckenaer. Subjects were deprived of their maintenance feeding of mealworms (*Tenebrio molitor* L.) for one week and then filmed during the capture of adult domestic crickets (*Acheta domesticus* L.). The spiders had a body length of 18.2 ± 1.48 mm ($n=10$); the crickets, 23.8 ± 1.87 mm ($n=10$), or about 30% longer than the spiders. Most of the spiders weighed 400-600 mg; the crickets, 600-1000 mg. Smaller spiders were offered smaller crickets within the size range; larger spiders, larger crickets. In most of the predatory sequences filmed, the prey were larger and heavier than the spiders.

For each film session I placed a spider into an all-glass arena, 100 mm in height, whose back wall was covered with paper to prevent reflection of light into the camera. The arena floor measured 80 mm front-to-back, 100 mm wide, and was covered with paper to provide traction. The arena's dimensions provided adequate room for interactions like that shown in Fig. 10, while yielding a film image with sufficient magnification and depth-of-field for later analysis. Each filming sequence was initiated when a cricket that had climbed out of a vial, which rested on the arena ceiling, fell through a hole into the arena. (In early attempts to film, I waited until the spider began to pounce before starting the camera and thereby missed part of the interaction.)

A Cine-8 Super-8 mm camera (Visual Instrumentation Corp., Burbank, California) (Model SP-1) and a Kinoptik 50 mm f/2 Macro-Apochromat lens were used. The camera was kept in a fixed position on the tripod. A pair of 500-W slide projectors, one on each side of the front of the arena, provided illumination. Using Kodak 4-X reversal film (ASA 400) and a lens setting of f/11, I was able to obtain sufficiently bright and sharp images at the maximum camera speed of 250 fps. Films were analyzed on a Kodak Ektagraphic projector (Model MFS-8). A total of 207 prey capture attempts on 36 reels of film were examined (176 of *L. rabida*, 20 of *L. aspersa*, and 11 of *L. helluo*). In addition, photographs were taken with the aid of two, synchronized, electronic flash lamps (Rollei E15B; flash duration = 1/2000 sec). Species photographed included the above three, as well as *L. punctulata* Hentz and *L. timuqua* Wallace. (As in the few *L. aspersa* studied, the individuals of *L. timuqua* were about as large as the crickets.)

To prevent experimental spiders from envenomating the prey, I applied melted paraffin to the flexed fangs of anesthetized (CO_2) spiders and sealed the fangs into the cheliceral grooves. (This was performed on three *L. rabida*.) When I also wished to prevent use of the chelicerae, these appendages were bound together with a distally placed cast of paraffin (Fig. 1). Three *L. rabida*, one *L. aspersa*, and one *L. helluo* received this combined treatment. Spiders so treated did not starve; each could still use its endites and labium to feed by scavenging on cut-up mealworms that I placed in their home cages.

Another type of experimental modification involved removal of the scopula hairs from the ventral and lateral surfaces of the tarsi and metatarsi of all the legs, and from the tibiae of the anterior two pairs. For each such operation I anesthetized the spider, inverted it, and "stapled" its body and legs to a styrofoam block with pairs of pins. Then, while observing it under a stereomicroscope, I shaved off the scopulae with a microscalpel. During the 2-3 hr of shaving, the spider occasionally struggled briefly to free itself, not being under anesthesia. The spiders subjected to this modification were those five that previously had been treated to prevent envenomation and use of the chelicerae; therefore, they had been filmed capturing prey prior to being shaved. Thus, the same individuals provided data for both the unshaven and the shaven conditions.

In analyzing the effect of scopula removal, I compared the unshaven vs. the shaven conditions on the basis of the number of prey escapes per total bouts of contact by the spiders. A 2X2 contingency table (Model I), using the *G*-statistic (Sokal and Rohlf 1969), served to test H_0 : prey retention is independent of the presence of scopula hairs on the legs. Throughout this paper, means are accompanied by S.D.'s.

RESULTS

I. Control spiders

Orientation Toward the Prey.—The spiders turned to face (and then approached) the prey in response to visual or vibratory cues. Spiders sometimes could respond visually to leaping crickets arcing above them by rapidly re-orienting to the moving target and capturing the insect as it landed. In response to vibrations induced by a cricket walking behind it, the spider performed one or more pivoting movements to face the prey.

In some cases the spider performed a sudden "pivot leap" to partly or completely face a cricket that had just landed behind it. This began with a synchronous spine erection on all of the spider's legs; the spider then twisted and raised the anterior end of its body as it lifted the anterior three pairs of legs. It twisted further and pushed with legs IV, the impetus of its pivot carrying the spider in a turn with all the legs now in the air, until a landing on the anterior three pairs of legs.

The Pounce.—Female *Lycosa* spp. could leap short distances to capture prey, such leaps covering about 1.5-2 body lengths of the spider. However, contact of legs IV with the substratum was lost for only about one body length, the leg IV tarsi sliding on the substratum for up to one-half of the leap, especially during the landing. In most captures the pounce was a response to prey within reach and did not involve such a true leap into the air; i.e., the leg IV tarsi maintained contact with the substratum throughout the pounce. The pounce in this case involved a push forward and obliquely upward, with the partly flexed legs I already raised into a high arch (and then legs II likewise); all of this resulted in lifting the spider's body to a position above the adjacent prey (Fig. 2).

In both types of pounces, while legs III sometimes may have contributed to the thrust, most of the propulsion was provided by legs IV. The activation of the hydraulic system needed to power the extension of these legs was reflected in the occurrence of synchronous spine erection in all the legs just prior to and throughout the pounce. Spine erection was first seen as legs I were raised (the first element of the pounce), which involved flexure of the trochantero-femoral and femoro-patellar joints. During the propulsive thrust, increased traction on the arena floor probably was provided by specialized scopula hairs on the plantar surfaces of legs III and IV (Type B leg scopula hairs, Rovner 1978).

Contact and Restraint.—Initial contact with the prey involved the distal ventral surface of the spider's legs I and II. After making contact, the spider pulled itself closer to the prey, an action requiring a firm hold by these anterior legs. With large prey, such as these crickets, legs III and then IV also were brought into contact, the eight legs forming a kind of "basket" that partly or completely surrounded the prey (Fig. 3).

Legs I and II continued to be the most important ones during the next portion of prey capture, since they served to position the spider's anterior end, thereby enabling the spider to bring its fangs into contact with the prey. The degree to which the less-used legs III and the least-used legs IV were employed depended on the activity level of the prey. Thus, in a struggle with a vigorously responding cricket, these posterior legs also were used both to restrain and to manipulate the prey; with less active prey, they were not used.

Since the cricket often kicked or pushed against the spider with its metathoracic legs, the loss of grip by one or more of the spider's legs was compensated for by the continued or renewed contact of its other legs. Even though the cricket often successfully thrust against the spider's sternum, abdomen, or proximal leg segments and thereby pushed the spider to a distance of a fully extended metathoracic leg, the spider did not lose contact with the prey. The spider was able to keep its tarsi (and perhaps metatarsi) pressed against the prey, the spider's legs being longer than the cricket's (Figs. 4 and 5).



Fig. 1.—Female *Lycosa punctulata* treated to illustrate the author's method of employing a paraffin cast (arrow) to prevent spiders from using their chelicerae and fangs.

Orientation on the Prey and Fang Insertion Sites.—During prey restraint, the spider typically had its body axis parallel to that of the cricket, spider venter against cricket dorsum. Since contact usually occurred as the cricket was moving away from the spider in an escape attempt, both animals faced in the same direction during capture in 88% of the cases (Fig. 6). To attain the final capture position, the spider pulled itself forward until its anterior end was near the cricket's thorax. Of the 51 captures in which both predator and prey faced the same direction, 26 fang insertion sites were in the thoracic region, 22 in the anterior abdomen, and 3 in the metathoracic leg (proximal segments). Of the 7 captures in which predator and prey were facing in opposite directions, 5 fang insertion sites were in the thoracic region, 2 in the anterior abdomen. Fang insertion sites in the thoracic and abdominal regions involved roughly equal proportions of dorsal, lateral, and ventral locations.

Inversion.—In preliminary trials on female *L. rabida*, 7 of 15 captures ended with the pair of animals inverted (Fig. 7). The inverted position was maintained for several minutes until the prey was immobilized by the venom. Then the spider regained an upright position by rolling to one side or forward while maintaining its cheliceral grip on the cricket.

That the inversion usually was due to the cricket's behavior was determined by observing the capture of crickets from which I had removed metathoracic legs. Only 3 of 15 captures involving crickets that lacked one leg ended in the inverted position. None of 20 captures involving crickets that lacked both metathoracic legs ended in the inverted position. During subsequent cinematographic studies, there were a few cases in which a capture ended in an inversion that was not caused by the metathoracic legs. Because of the basket-shaped configuration of the spider's legs when grasping large prey, a rolling of the spider (with its prey) resulted from the momentum of the pounce.

Metathoracic Legs of the Cricket.—Frame-by-frame analysis of prey capture behavior revealed the cricket's use of its jumping legs. These long, powerful appendages could be rotated at the base to aim in most directions in both the horizontal and vertical planes.



Fig. 2.—Female *Lycosa timuqua* about to pounce on a cricket (*Acheta domesticus*). Three of the spider's four anterior legs are raised.

They often were used in a directed manner, being aimed—even anteriorly—toward the spider during wrestling. The spines on the cricket's metathoracic legs sometimes engaged the spines on the legs of the spider, thereby improving the effectiveness of the thrust. Typically the cricket extended both legs synchronously, unless the movement of one of them was restricted by the spider.

When the spider was above the cricket and the cricket was upright, the latter's metathoracic leg thrusting against the substratum propelled both animals into a semi-elliptical trajectory through the air. In six filmed examples that could be measured, the pair of animals reached a height (taken as the distance from the spider's eyes to the substratum) of 37 ± 8.2 mm, the highest being 48 mm (about 2.7 body lengths of the spider). These "flights" lasted 0.15 ± 0.03 sec, as timed from the loss of contact with the substratum to renewed contact (Figs. 8, 9, and 10).

A series of several, synchronous, metathoracic leg thrusts sometimes occurred while the animals sailed through the air. The components of each thrust were executed very rapidly; e.g., from the fully extended position back to the maximally flexed position took only about 0.02 sec. Leg thrusts occasionally were effective in dislodging one or more of the spider's legs or in pushing the spider's body away, thereby temporarily loosening the grasp (Fig. 10g). The spider responded instantly to such actions by renewing contact of its just-dislodged legs or initiating a re-positioning of its body, i.e., a change in its orientation on the cricket. All of this occurred in flight while the spider clung to the prey. Rarely did these spiders lose total contact with the prey due to the latter's actions. Thus, the pair of wrestling animals traveled the entire trajectory as a unit.

Contact Surface of the Spider's Legs.—Throughout all of the above-stated events, the spider used its distal leg surfaces for contacting the prey. (The palps were not used in prey capture.) Thus, rather than tightly enclosing the prey and pressing against it with the entire ventral surface of its legs, the spider used the scopula-covered portions of the legs and often kept its body at a distance from the struggling cricket until fang insertion was attempted. The scopula hairs were erect during capture.

Two aspects of prey capture revealed in the films indicated the firmness of the plantar surface's grip: (1) Spiders were able to use one of their tarsi to hold onto the cricket's thrusting metathoracic leg; contact was maintained without slipping on the rapidly shifting substratum provided by the jumping leg. (2) Spiders could pull themselves forward and regain a position juxtaposed to the prey after the cricket had partially escaped from the spider's grasp. During mid-air interactions, after the cricket had leaped, the spiders were able to pull themselves upward onto the cricket from a position in which they had been hanging from the cricket.



Fig. 3.—Female *Lycosa timuqua* enclosing a struggling cricket in a "basket" of legs. Note the spider's use of the distal leg segments for contact. (Exposure=1/2000 sec).

Film analyses showed a very minor role for the tarsal claws in prey restraint. Occasionally during a struggle, the claws on one or two of the spider's legs would engage joints or spines on the cricket's legs, thereby restricting movement of the latter to some degree.

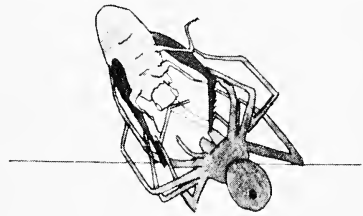
Events After Fang Insertion.—Soon after the spider succeeded in inserting its fangs and grasping the prey in its chelicerae, the spider removed most or all of its legs from contact, especially if in the inverted position. If above the prey or leaning back behind it, the spider extended legs I and II away from the prey. Contact by the legs was renewed briefly only to manipulate the prey or to restrain additional movements that preceded immobilization.

Even after envenomation had occurred, a lack of restraint of the prey prior to immobilization could result in its loss; consequently, the cheliceral grasp was maintained for a number of minutes until struggling ceased. Thus, feeding on large prey could begin only after the venom had immobilized it. In some cases, post-immobilization prey wrapping (Rovner and Knost 1974) also occurred prior to ingestion.

II. Experimental Spiders

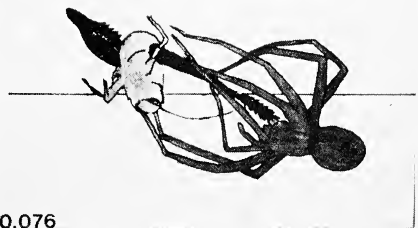
Modified Fangs.—Spiders deprived of the use of their fangs (by having them sealed into the cheliceral grooves) still were capable of using their chelicerae to hold the cricket firmly. These muscular, toothed appendages were pressed together into the prey's body and provided a secure hold sufficient for restraint of a jumping cricket, without the need for continued leg contact by the spider. Such "de-fanged" spiders wrestled with the prey for over 1 hr, being unable to immobilize the prey in order to begin feeding. Every time that the cheliceral grip was relaxed, the cricket began to escape and had to be restrained once more, first with the spider's legs and then with its chelicerae.

Modified Chelicerae.—Spiders unable to use their chelicerae (due to a paraffin cast) had to maintain leg contact at all times in order to restrain the prey. Thus, such spiders'



0.000

Fig. 4.—Diagrams based on a film (recorded at 250 fps) of a female *Lycosa rabida* manipulating a struggling cricket. Although the cricket pushed its right metathoracic leg against the spider's sternum (lower diagram), the spider's longer legs enabled it to maintain contact with the prey and subsequently pull it back to a more proximate position. Elapsed time (sec) is at the lower left.



0.076

behavior was unlike that of untreated animals or of those with modified fangs, both of which extend their legs away from struggling prey as soon as a firm cheliceral grasp is achieved.

Shaven Spiders.—Removal of scopula hairs from the legs reduced but did not altogether eliminate the ability of the spiders to restrain crickets. The attempt to grasp the prey after making initial contact with legs I and II sometimes failed, especially if the cricket leaped in response. This may have been due in part to the tarsi slipping on the substratum during the approach (especially the leg IV tarsi that provide the thrust for the pounce), as revealed in the films. However, it was evident in many cases that the plantar surfaces of legs I and II had been pressed against the prey but slipped over the surface of the body rather than maintain a firm contact. In other cases, shaven spiders succeeded in at least establishing a temporary leg basket around the prey.

Although shaven spiders often could hang onto crickets during leaps by enclosing them in a leg basket, they were less able than unshaven ones to maintain control of struggling prey throughout the trajectory, especially if the cricket's metathoracic legs pushed against the spider. Thus, leg thrusting by the prey more often resulted in escape from shaven spiders than from unshaven ones. The data indicated a significant dependence ($G = 39.474$; $P < 0.001$) of the ability to restrain prey on the presence of leg scopula hairs. Shaven spiders lost the prey in 78 cases, more than twice as many times as they retained it (35 cases); while control spiders retained prey in 69 cases, nearly three times as often as they lost it (24 cases).

DISCUSSION

Data collected in this study indicate that the morphology of lycosid spiders reflects various adaptations that function in prey capture. Some of these specializations—adhesive hairs, a preponderance of flexor muscles in the legs, and leg length—also serve locomotor



Fig. 5.—Female *Lycosa rabida* inverted on the substratum and using the tips of its fully extended legs to manipulate a struggling cricket that was thrusting its metathoracic legs against the spider. (Photograph of a frame of Super 8 mm film exposed at 250 fps).

needs. Others—powerful chelicerae, a venom apparatus, and erectile spines—evolved specifically for predatory interactions. While lycosids were the subjects used here, many of the hypotheses discussed below are applicable to members of most families of wandering spiders.

Adhesive Hairs.—A locomotor role for the leg scopula hairs had been hypothesized by Homann (1957) and supported by Foelix and Chu-Wang (1975). A predatory function for these hairs (in addition to the locomotor one) was hypothesized by Rovner (1978), based on a survey of their distribution on the legs of diverse wandering spiders and their absence in web-weavers. The experimental approach in the present study has yielded support for both hypothesized functions. Shaven spiders tended to slip more than non-shaven ones as they attempted to move quickly over the substratum during prey capture. Likewise, shaven spiders showed a reduced ability to restrain prey from escape. Unfortunately, the experiment is confounded by the loss of sensory hairs due to shaving; their absence may have altered the ability of the spider to monitor pressure applied to a substratum.

The finding that unshaven spiders could restrain large crickets for prolonged periods by use of the distal leg surfaces alone, i.e., without the aid of chelicerae or fangs when so treated, provided further support for the hypothesized role of the adhesive hairs in predation. On the other hand, the ability to restrain prey was not eliminated entirely by shaving off the leg scopulae, indicating that these structures are not essential for this function. Thus, as with many morphological adaptations in animals, the adhesive hairs improve the effectiveness of a system but are not indispensable for some degree of success.

Acquisition and manipulation of the prey by the spider depended primarily on the anterior two pairs of legs. Effective traction was important for a successful landing on the cricket during a pounce, the initial contact being a critical point in the capture sequence. Subsequent restraint and manipulation of large prey usually involved the distal plantar surfaces of all four pairs of legs, the exclusive sites of the adhesive hairs. It is possible that the evolution of these hairs in wandering spiders related mostly to their role during predation on large or powerful prey, particularly those that could escape by leaping or flying. The natural prey of various lycosids, for example, includes grasshoppers, crickets, and other orthopterans, as well as adult lepidopterans and dipterans (Kuenzler 1958; Whitcomb and Bell 1964; Edgar 1969). Correspondingly, the jumping and flying abilities of the ancestors of such insects probably were, in part, evolutionary responses to predation by ancestral wandering spiders. Thus, we may have here a crude example of coevolution in a predator-prey relationship.

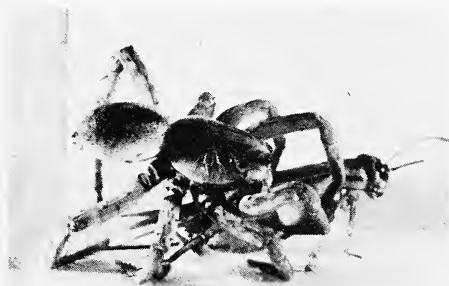


Fig. 6.—Female *Lycosa timuqua* attempting to restrain an escaping cricket just after the capture sequence was initiated. Note that both animals face in the same direction. The spider subsequently pulled itself forward to the typical, more anterior location in which its "leg basket" enclosed the prey. (Exposure=1/2000 sec).

Leg Flexor Muscles.—Closely associated with the localized gripping function of the adhesive hairs is the overall grasping ability of the spider imparted by the predominance of flexor muscles in the legs. The importance of this feature of spiders for prey capture was suggested by Anderson and Prestwich (1975). In the present study, the ability of unshaven spiders to restrain struggling crickets with the tips of the spider's fully extended legs (Figs. 4 and 5), and the ability of shaven spiders to partly restrain struggling crickets without the aid of the chelicerae or fangs, both provide evidence for the Anderson and Prestwich hypothesis: the spider's peculiar muscle arrangement—legs packed with flexors—is an adaptation yielding maximum grasping strength for prey capture.

Hydraulic System.—Shifting to a preponderance of flexors for prey capture meant having a dearth of extensors, which Anderson and Prestwich (1975) hypothesized led to the need for a hydraulic mechanism to provide for efficient leg extension. The importance of this feature was seen in two aspects of prey capture: (1) The propulsive force of the spider's leap or pounce depended mostly on the sudden extension of legs IV, a lesser version of that action described for a salticid spider by Parry and Brown (1959). The great increase in hydrostatic pressure just prior to the leap was indicated by the synchronous erection of the leg spines. (2) Spine erection continued throughout the time that the legs were used for grasping during the prey's struggling. The maintained high level of hydrostatic pressure enabled the spider to extend the legs rapidly, an important ability because of the need to move the legs away from the powerful kicks of the cricket's spiny metathoracic legs. Rapid leg extension also occurred during manipulation of a struggling prey, the leg first being lifted away and then placed at another site on the prey. Thus, during prey capture, high levels of activation of both the leg flexor muscles and the hydraulic mechanism for leg extension are occurring.

Erectile Spines.—Throughout most of the lycosid spider's life, the large spines rest against the leg surface, thereby not interfering with locomotion of the animal through narrow spaces in the physical structure of the environment, as would permanently erect spines. When the spines are erected, they probably make it difficult for an opponent to get close enough to the leg surface to injure the spider. In turn, the now spiny legs can be used to keep the opponent safely away from the spider's body. Only twice in all of the filmed encounters did a cricket succeed in biting the spider, in both cases on a distal leg segment. (In response, the spider immediately released the prey from its grasp.)

This view of a defensive function for the erectile spines supports the original hypothesis of Gaubert (1892) but disagrees with that recently proposed by Harris and Mill (1977). The latter workers regard these spines as "haemocoelic pressure monitors" and suggest that any defensive role is secondary "since the danger inflicted by an erecting spine would be minimal." However, Harris and Mill themselves point out that the spines

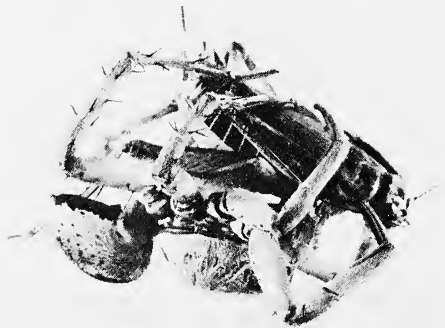


Fig. 7.—Female *Lycosa timuqua* lying inverted on the substratum after capturing a cricket.

are much larger than they need be for a receptor function. Furthermore, erection is maintained throughout two dangerous activities—prey capture and fighting with conspecifics (Rovner 1968). Finally, many spiders (e.g., oxyopids) only have permanently erect large spines (Gertsch 1949), yet presumably also must monitor hydrostatic pressure. Thus, I regard the erectile spines as defensive structures, whose receptor units provide information about the rate and degree of erection. Such information therefore can be monitored independently of other hydraulically mediated actions, such as erection of the adhesive scopula hairs (Rovner 1978), which accompanies spine erection during capture.

Leg Length.—While locomotor needs provide an important selective pressure in the evolution of leg morphology in wandering spiders, observations in the present study suggest that predatory needs play a part as well. Just as specialized leg lengths have evolved in certain spiders (e.g., thomisids) for particular methods of capture, the range of suitable leg lengths in the more generalized forms (e.g., lycosids) may be influenced by the need to combine grasping strength with the ability to keep the body at a safe distance from the weapons of dangerous prey.

Chelicerae.—Lycosids prevented from using their fangs still were able to restrain crickets by holding them with the chelicerae, even without the spider using the legs, once a firm cheliceral grip had been established. Thus, at some point in capture, these dentate appendages take over the function of restraint from the legs, which then are extended away from the prey and thereby removed from potential danger. Of course, in untreated spiders the fangs are driven into the prey's body by the chelicerae and provide additional aid in gripping the prey. Indeed, the fangs of spiders may have evolved from tooth-like precursors that served only for gripping in some non-venomous ancestral form.

Venom Apparatus.—While the chelicerae alone enabled the spider to restrain large prey, they did not suffice for the utilization of such prey, since ingestion required prey immobilization. Spiders experimentally prevented from using their fangs were unable to



Fig. 8.—Female *Lycosa timuqua* wrestling with a cricket as both travel in a trajectory. The pair were catapulted upward by the cricket's metathoracic legs thrusting against the substratum. (Exposure=1/2000 sec).

begin feeding on large prey. Thus, for "de-fanged" spiders, capturing prey was not equivalent to acquiring a meal; the prey merely was held in check.

Enders (1975) had pointed out the lack of any experimental study that "demonstrates by how much a venom increases the upper limit of size of prey that is taken." The technique developed for the present study—sealing the fangs or the chelicerae—furnishes a suitable approach to this problem. Able to use the chelicerae but not the fangs, spiders can capture but not feed upon large prey. Thus, the venom apparatus does increase the upper limit of prey size taken, in that it enables the spider to begin ingestion. (For small prey, the chelicerae alone are sufficient for immobilization.) A quantitative answer to Enders' question of the size increase of the prey that venom provides for the spider would require presenting an array of prey sizes and types; nevertheless, the qualitative finding of my study does support his hypothesis. Thus, it is likely that the advantage of greater prey biomass per capture was the factor that produced the selective pressure for the evolution of the venom apparatus in spiders.

Prey Morphology.—While many caterpillars, flies, and other prey of lycosid spiders present no hazard, the cricket is potentially dangerous. Riechert (1973) reported that similar prey (locustid orthopterans) could use their metathoracic legs to perforate the soft integument of agelenid spiders when struggling took place in the confines of the funnel. While no such injuries occurred in the relatively open arena use in the present study, it is likely that capture attempts beneath objects or within the interstices of dense plant material near the ground would involve a similar danger to lycosids. Much (perhaps most) of the selective pressure for the evolution of the spines and musculature of these orthopterans' metathoracic legs probably came from predation by spiders.

Prey Size.—The prey used in my study usually were as large or larger than the spiders; furthermore, the prey were not defenseless. This refutes the assertion by Enders (1975)



Fig. 9.—Female *Lycosa aspersa* using its distal leg segments to hang onto a cricket as both travel in a trajectory initiated by the cricket. (Exposure=1/2000 sec).

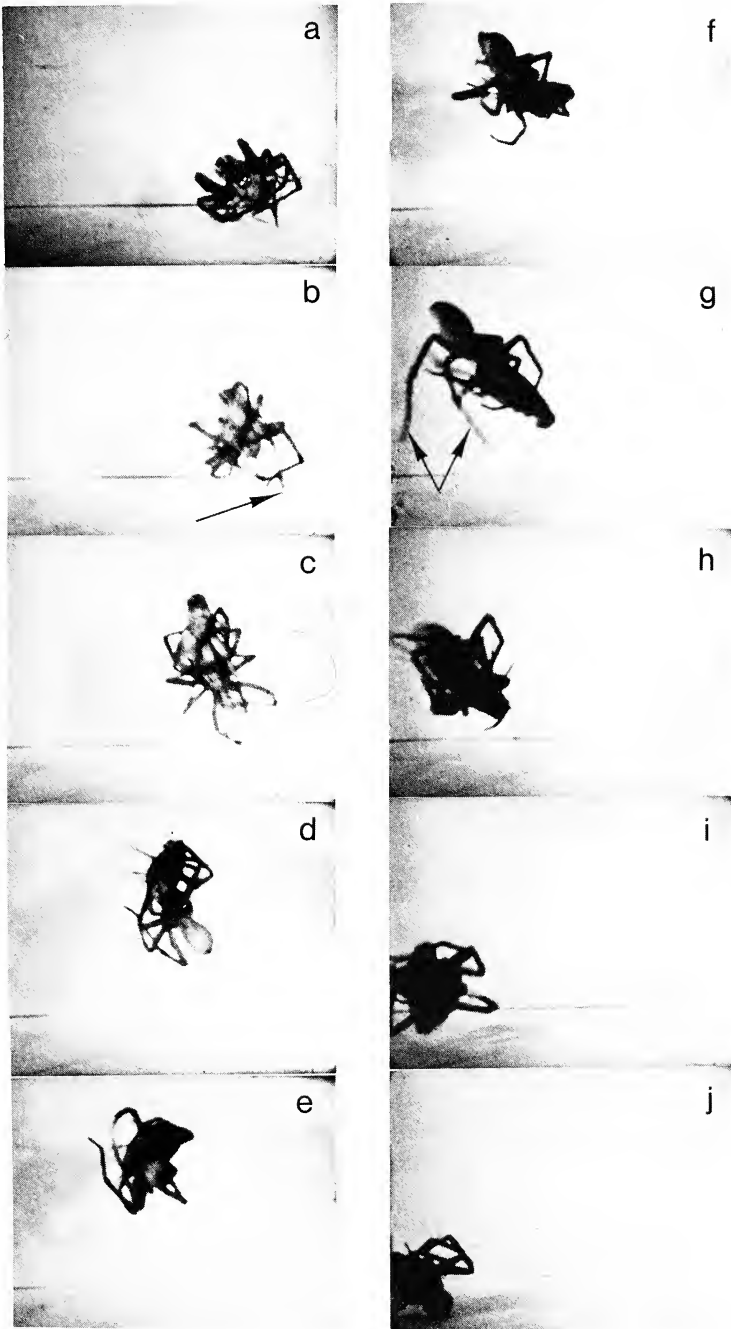


Fig. 10.—Female *Lycosa rabida* travelling in a trajectory with a struggling cricket, as recorded on Super 8 mm film at 250 fps. Every fifth frame of the film is shown; thus, the interval between pictures is 0.02 sec. The total sequence lasted 0.18 sec. In a-c the cricket's left metathoracic leg (arrow) thrusts against the substratum and lifts both animals obliquely upward. During d-f the zenith is reached (about 35 mm above the substratum), as the animals roll to a position with the spider above the cricket. In g the cricket's metathoracic legs thrust outward, dislodging the spider's right legs III and IV (arrows). In h the spider has returned these legs to contact with the prey. Impact with the substratum occurs in j.

that "terrestrial temperate-zone nonweb spiders of greater body weight (Lycosidae) are not reported to capture large prey." Enders was seeking to support his hypothesis that "the use of silk by the web spider is demonstrably the use of a tool or net to subdue larger (or more difficult) prey than the nonweb spider can handle." Observations herein, as well as those of Robinson and Valerio (1977) on salticids and of Whitcomb et al. (1966) on oxyopids, indicate that nonweb spiders readily capture large and often dangerous prey. Thus, Enders' hypothesis that webs arose as tools to increase the upper limit of size of prey is in doubt.

Family-specific Capture Behavior.—Patterns common to most of the interactions that were filmed suggested that there is a "lycosid style" of capturing large, dangerous prey. The pounce, while over a shorter distance than that of a salticid or oxyopid spider, likely gives lycosids a greater range of effectiveness than those wandering spiders that do not pounce. After contacting the prey, repeated re-positioning to avoid defensive weapons may represent a tactic that certain other wanderers (e.g., thomisids) do not include in their repertoire. The aggregate of behavioral elements available to each kind of spider for predation probably influences the success of capturing certain types of prey and, in turn, delineates this aspect of the spider's niche. While this aspect has been well-studied in web weavers, the wandering spiders have received little attention.

Studies of heteropodid and oxyopid spiders (Rovner, unpubl. data) likewise reveal predatory behavior that is probably characteristic for the family or perhaps even a lower taxon. While lycosids (Edgar 1969; Ford 1978), heteropodids, and oxyopids (Whitcomb and Bell 1964) are usually "sit-and-wait" predators, how and where the spider "sits," as well as how it contacts, restrains, and manipulates the prey, are different among the families. It is likely that the differences affect the kinds of prey captured. This brings into question the concept of a single "guild of wandering spiders" that some authors (e.g., Uetz 1977) have used in lumping these diverse spiders into a category implying a similar manner of resource exploitation. It seems more appropriate to follow Enders' (1975) viewpoint: Within each of the three major modes of hunting (which were originally suggested by Gertsch 1949)—short-sighted wanderers, long-sighted wanderers, and web spiders—there exist a number of guilds characterized on the basis of both hunting manner and prey type used. Indeed, one wonders if Post and Riechert's (1977) division of the wandering spiders of Tennessee forests and fields into only four guilds—diurnal runners, nocturnal runners, crab, and jumping spiders—represents a sufficient separation of wanderers comparable to the seven guilds of web dwellers that these authors appropriately distinguish. Future research may support the idea of several guilds, each definable in part by a unique combination of behavioral elements that constitute the predatory repertoire, within each of the present diurnal and nocturnal runner categories.

Complexity of the Nervous System.—The cinematographic analyses of Melchers (1967) and of the present study suggest another aspect of the predatory behavior of various wandering spiders—their extraordinarily rapid and complex responses to the prey's actions. (Melchers' finely tuned analysis includes data on the speed and complexity of predatory elements in the ctenid *Cupiennius salei*.) Compared to these spiders, the well-studied behavior of the mantis is simple—"aim and shoot." Unlike the latter insect, lycosid spiders must make many varied responses using most or all of their appendages during a brief interaction to secure the prey. This requires a nervous system that can make rapid analyses of an ever-changing stimulus situation in order to yield output that provides for continued control of the struggling prey while simultaneously adjusting the spider's position to reduce the possibility of injury from the prey's weapons.

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THE MATING STRATEGY OF *PHIDIPPUS JOHNSONI*
(ARANEAE, SALTICIDAE):
II. SPERM COMPETITION AND
THE FUNCTION OF COPULATION

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ABSTRACT

The number and sequence of individual palp applications during copulation were highly variable. Copulation duration was correlated with different mating tactics: a. adult female outside nest, type 1 courtship (vision dependent), copulate outside nest (mean duration: 14 min); b. adult female inside nest, type 2 courtship (vibratory), copulate inside nest (110 min); c. subadult female inside, cohabitation, copulate inside nest after maturation of female (863 min). Females were more likely to oviposit fertile eggs after long copulations; but given that any fertile eggs were oviposited, there was no evidence that the number varied with copulation duration. Female fidelity (the probability that she would not mate when another male courted her) was greater after longer copulations. When females became unreceptive after mating, the effect was nearly immediate. Males covered the copulatory orifices of females with mating plugs that apparently hindered insemination attempts by later males. Females that mated with more than one male included some that were capable of ovipositing fertile eggs after their first copulation. The sterile male technique (x-radiation) was used to investigate the consequences of repeated mating. Sometimes the second male failed to displace any of the first male's sperm. Other times, there was partial or complete displacement. Possible mechanisms controlling female receptivity and their adaptive significance are discussed.

I. INTRODUCTION

Very lengthy copulations occur in many animal groups. For example, some species of crustaceans and insects may remain *in copula*, without interruption, for hours or even weeks at a time (Hartnoll 1969, Nayar 1958, Richards 1927, Unwin 1920). At the opposite extreme, copulation lasts for only a few seconds in some Diptera (Corbet 1964, Syrjamäki 1966). Comparable variance among species occurs in the copulation durations of spiders (Bristowe 1958). There is also variation among species in the details of copulatory behavior. For example, there may or may not be repeated mounting or the formation of locks; and the male and female may assume various positions relative to each other, such as facing the same or opposite directions and the male dorsal or ventral to the female (Gerhardt and Kaestner 1937, Richards 1927). To understand interspecific variation in copulatory behavior apparently requires consideration of functions in addition to the simple transfer of sperm from the male to the female.

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In species in which females copulate with more than one male, sperm competition often occurs (Parker 1970). In competition of this type, the female's eggs are a limited resource for the males. As the proportion of her eggs fertilized by one male's sperm increases, the proportion fertilized by the sperm of other males decreases. Many aspects of the reproductive biology of animals can be viewed as adaptations related to this type of competition. Although sperm competition has rarely been considered in studies of spiders, arguments concerning particularly intense sperm competition in insects probably apply to spiders as well, since a single male ejaculate may be adequate to match the female's semen storage capacity and fertilize all her eggs.

In the salticid spider *Phidippus johnsoni* Peckham and Peckham, there is a surprising degree of intraspecific variation in copulatory behavior. In particular, the duration of copulation varies within this species over a range approaching that which occurs in the animal kingdom as a whole. This extraordinary variance in copulation duration is correlated with the alternative mating tactics employed by the males of this species (Jackson 1977a):

- (1) Courtship occurring outside the nest tended to be followed by copulations lasting only a few minutes.
- (2) Courtship involving females encountered as adults inside nests tended to be followed by copulations inside nests lasting as long as several hours.
- (3) Following cohabitation, copulations with newly matured females tended to be extremely lengthy, frequently lasting longer than a day.

Previously the pursuit times (courtship and cohabitation durations) associated with each tactic were discussed (Jackson 1978a). In this paper the significance of copulatory behavior in the mating strategy of *P. johnsoni* will be considered.

Although Edwards (1975) reported that males of *Phidippus regius* C. L. Koch may terminate copulation by leaping off the female and running away, this was never witnessed in the case of *P. johnsoni*. Instead, copulation was always terminated by the female. For example, females dislodged males by walking or turning in circles, and they drove males away by striking at them with their forelegs, charging toward them, or pushing them (Jackson 1977a).

With respect to the females, the issue of interest is the adaptive significance of variance in how long they tolerate copulating males. This will be a primary concern in Sections III and X. For the male, the question of interest concerns the adaptive significance of prolonged copulation, since each male apparently attempts to copulate for as long as possible. This question will be dealt with especially in Sections IV, V, VI and IX.

General information concerning the maintenance and observation of spiders is provided elsewhere (Jackson 1978a). All statistical tests are described by Sokal and Rohlf (1969); and unless otherwise noted, data are given as means \pm S.D.'s. Whenever it was necessary to select spiders for observations in the laboratory, this was usually done randomly (random numbers table, Rohlf and Sokal 1969) or occasionally haphazardly (i.e. with no conscious choice, but not using a random numbers table).

II. PATTERN OF COPULATORY BEHAVIOR

Introduction.—During copulation, both inside and outside nests, the male and female of *P. johnsoni* faced opposite directions with the male's ventral surface against the female's dorsal (mating posture No. 2: Gerhardt and Kaestner 1937). The palpal organs were applied one at a time, the right palp to the right copulatory orifice of the female and

the left palp to the left orifice. While copulating the male leaned to one side of the female, and the female's abdomen rotated 45° to 90° . Between each successive palp application the female's abdomen rotated back to its normal position, and the male tapped and stroked with his legs and palps. Sometimes copulation was interrupted by periods during which the male was not mounted, during which time he might be inactive, groom or perform other activities seemingly not related to communication. However, the majority of the time during which the male was not copulating was spent courting (Jackson 1977a). During transfer of semen, the male's embolus must enter the female's copulatory orifice; but I was unable to observe this during the present study. Consequently, copulation was defined simply as times during which the male's palpal organs were in contact with the epigynum, also referred to as palp "application" or "engagement." Pulsations of the hematodocha occurred throughout the durations of even the longest palp engagements. A single "copulation" was usually comprised of more than one individual application.

Number of Palp Applications.—The number of palp applications per copulation was not related in any simple way to the duration of the copulation or whether the spiders were inside nests. Considering copulations for which numbers of applications were recorded precisely by means of continual observation (Fig. 1), copulations inside and outside nests did not differ greatly (Mann-Whitney U-test, n.s.) in numbers of applications, although copulation durations were very different (means: outside nest, 8.6 min; inside nest, 39.9 min; Mann-Whitney U-test, $P < 0.001$).

Considering copulations observed continuously, it was not unusual for lengthy ones to be accomplished with few palp applications: e.g. 5.85 hr (1 application); 6.00 hr (2); 8.85 hr (4) (each inside nest). Single palp applications lasted from 20 sec to as long as 7.42 hr, with applications lasting 1 or 2 min being common. Although there were copulations lasting 3 min involving 3 applications and 2 min copulations with 2 applications, all copulations lasting 1 min or less included but a single palp application.

Generally only a portion of each copulation following cohabitation was observed. One lasting 18.20 hr was observed in its entirety, during which there were 12 applications (duration for single application: 1-340 min). The maximum number of applications observed during a single copulation was 64 during one following cohabitation that was not observed in its entirety (observed duration: 8.15 hr; estimated: 10 hr).

Duration of Palp Applications.—Durations of individual palp applications followed no obvious rules related to the durations of preceding and following applications, whether palps were applied alternately or repeatedly, whether the application was early or late in the copulation, or whether activity by the female preceded disengagement (Fig. 2).

Sequence of Palp Applications.—Considering 923 cases in which males disengaged their palps and then re-engaged, the relative frequency with which the next application was made with the opposite palp was 0.82; that for the same palp was 0.18. The female's behavior was a factor influencing whether the male alternated palps or re-applied the same one. Whenever scraping on the female's abdomen (a component of postmount courtship: Jackson 1977a) followed within a few seconds of palp disengagement, the next engagement was on the opposite side. Sometimes the female's abdomen did not rotate and the male alternately scraped on one side, then the other; and the side on which he finally engaged his palp could be either the same or the opposite from his previous engagement.

Handedness.—There was a tendency for males to favor the left palp when starting to copulate, and there was evidence that individual males were either left or right "handed."

Considering 190 copulations in which the male scraped on only one side of the female's abdomen before the first palp engagement, the first palp applied was the left in 66.8% ($G = 21.985$, $P < 0.005$).

There were 33 males for which the first palp applied was recorded on two successive copulations, with each case preceded by scraping on only one side of the female's abdomen. Twenty applied the same palp first each time (16 left, 4 right). However, these frequencies were not different from those expected from the binomial distribution with equal probabilities for use of each palp. For another set of 15 males, the first palp applied was recorded on 3 successive copulations, with each preceded by scraping on a single side of the female's abdomen. Ten initially applied the same palp during each of the 3 successive copulations (9 left, 1 right). The null hypothesis of equal probabilities for initial use of each palp is rejected ($G = 11.507$, $P < 0.005$). Similar observations were available for 4 successive copulations of only 2 males, and neither initially favored the same palp during each copulation. The significance of "handedness" in the mating behavior of *P. johnsoni* is unclear (see Dill 1977 for a discussion of "handedness" in animals).

Comparison of Copulation with Courtship.—Although it is useful to define courtship as heterosexual communicatory behavior that forms the normal preliminaries to mating (Jackson 1977b), the temptation to assume a clear functional distinction between courtship and copulation can be misleading. For example, the copulatory behavior of the linyphiid spider *Lepthyphantes leprosus* consists of a lengthy first phase during which no sperm is transferred, followed by a shorter phase associated with insemination (van Helsdingen 1965). If the first phase has a communicatory function, it becomes problematic to decide whether this phase should properly be referred to as copulation, courtship, or both. There is increasing evidence that copulatory behavior in animals

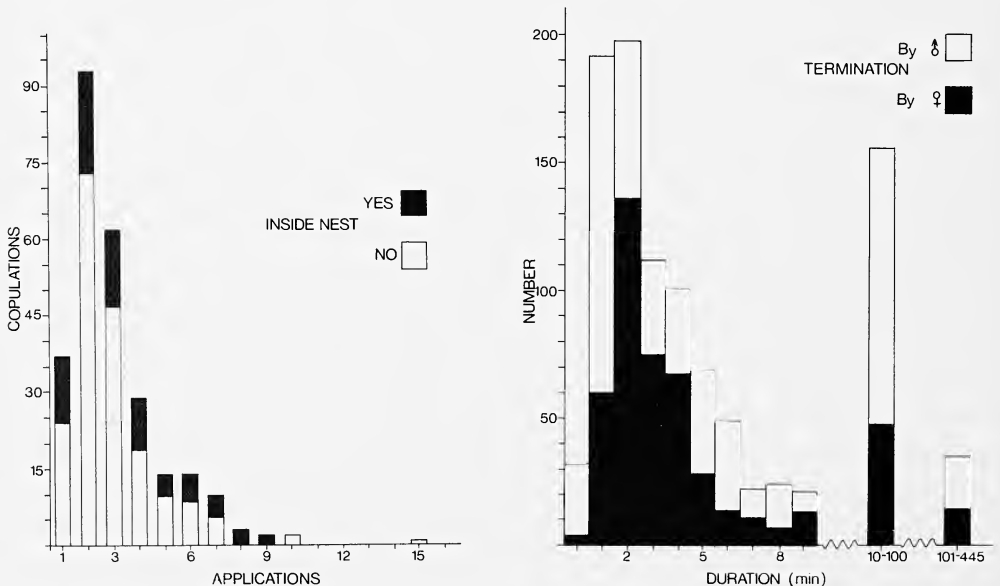


Fig. 1.—Number of copulations during which different numbers of palp applications occurred.

Fig. 2.—Durations of individual palp applications. Terminated by female: female becomes active just before palp removed from epigynum. Terminated by male: female inactive just before removal of palp. 0: 20 sec; 1: 40 sec or 1 min; 2: 2 min; etc.

sometimes serves communicatory functions analogous to courtship. For example, in certain mammals intromission patterns have communicatory functions, promoting fertilization and implantation and possibly enhancing reproductive isolation between species (see Dewsbury 1975).

The copulatory behavior of *P. johnsoni* is highly variable with respect to the number, duration, and sequence of palp applications. The sequence of behavioral units during courtship in *P. johnsoni* is highly variable also; and factors that might favor variability, such as reduction of monotony, have been discussed elsewhere (Jackson 1977a). If copulatory behavior has a communicatory function analogous to courtship, similar selection pressures may promote variability.

III. FACTORS AFFECTING COPULATION DURATION

Introduction and Methods.—Copulation duration was measured as the total time (to the nearest minute) during which the palps were applied, excluding intervening time occupied by other activities. Most copulations were observed virtually continuously; however, for 90 of the very lengthy copulations (Table 1, 1 from row 1; 8, row 2; 81, row 3), there were periods during which the pairs were not under observation, primarily during the dark period in the light regime of the laboratory (12 L: 12 D). One of these copulations took place outside the nest, and it will be discussed separately. The other 89 were inside nests. For each of these, an estimate was made of the fraction of the time spent

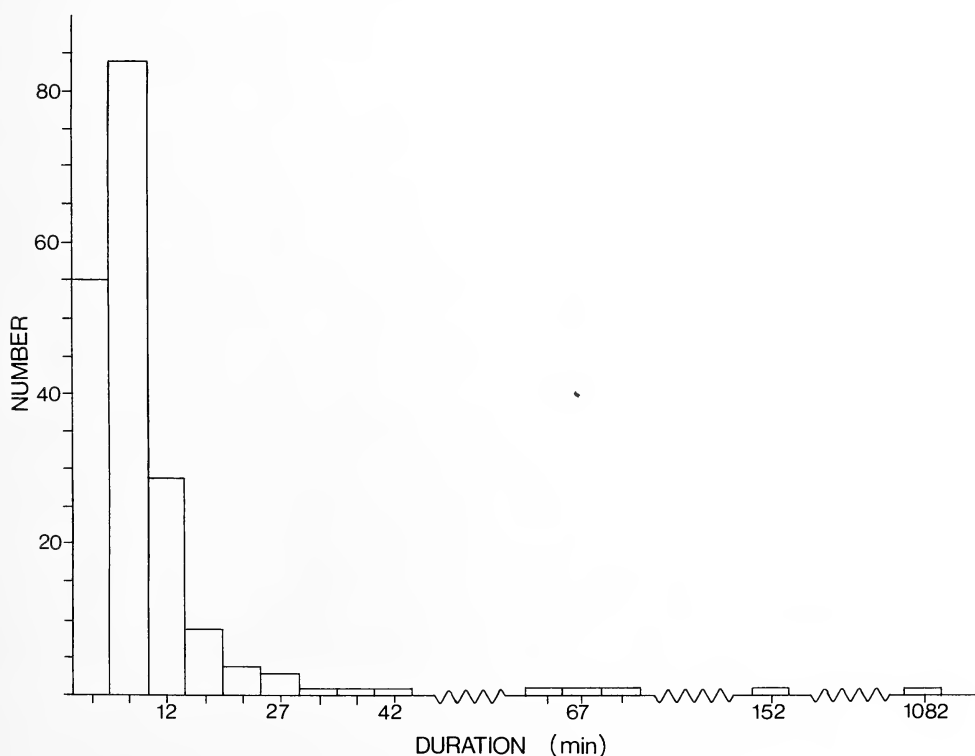


Table 1.—Durations (minutes) of different types of copulations (see text for details concerning each type). Two values for Mean and Max. given when each copulation not observed in its entirety: first, based on estimates; second, only the actually observed portions of each copulation. Outside and Inside: female outside or inside her nest when encountered by male. Cohabit: copulation preceded by cohabitation. Virgin: female's first copulation. Vegetation: copulation took place in presence of vegetation. Red Light: entirety of copulation occurred under incadescent light with red filter. Regular Light: at least part of copulation occurred under fluorescent light with no filter (copulations involving females that molted the same day excluded). Maternal: female inside her nest with eggs. Receptive, Second Day: durations of first copulations of females that were receptive on second day; Gravid: receptive on second day and/or when gravid; Maternal: receptive on second day, when gravid, and/or when maternal (inside and/or outside nest). Unreceptive, Gravid: unreceptive on second day and when gravid; Maternal: unreceptive on second day, when gravid, and when maternal (inside and outside nest). Plug formed: plug present after but not before the copulation. No Plug Formed: plug absent before and after. Enduring Plug: same plug present after at least one later copulation by a different male. Plug Endured and Plug Not Endured: a plug present previous to the copulation and same plug either present or absent afterwards.

Type of Copulation	Mean		Max.		Min.	N
1. Outside	14.13,	8.56	1078,	152	0.33	192
2. Inside, Not Cohabit	109.62,	85.63	1200,	843	0.66	114
3. Inside, Cohabit	863.33,	571.92	2400,	1336	6	89
4. Outside, Virgin, No Vegetation	8.63		152		0.33	109
5. Outside, Virgin, Vegetation	6.16		12		0.33	15
6. Inside, Virgin, Regular Light	51.38,	40.15	1200,	762	2	39
7. Inside, Virgin, Red Light	125.75		531		6	12
8. Inside, Maternal	217.36,	142.12	840,	517	1	25
9. Receptive, Second Day	93.87,	77.71	1680,	1228	0.33	52
10. Unreceptive, Second Day	571.00,	381.96	2400,	1336	1	100
11. Receptive, Gravid	261.48,	186.09	1920,	1228	0.33	49
12. Unreceptive, Gravid	633.79,	431.82	1920,	1158	2	68
13. Receptive, Maternal	341.38,	235.38	1800,	1158	2	21
14. Unreceptive, Maternal	793.33,	535.45	1320,	975	61	9
15. Plug Formed	402.68,	287.21	2400,	1336	1	132
16. No Plug Formed	317.47,	228.57	1680,	1228	0.33	32
17. Enduring Plug Formed	269.52,	188.71	1320,	975	3	21
18. Non-Enduring Plug Formed	247.08,	164.90	2400,	1336	1	48
19. Plug Endured	9.28		70		0.33	22
20. Plug Did Not Endure	123.25,	84.27	1078,	708	1	51

copulating when the spiders were not under observation. This was always less than 0.5, which was likely a conservative estimate in each case.

Observing under red light, I confirmed that *P. johnsoni* copulated during the dark period. In some cases, pairs that had been copulating during the day were checked intermittently during the night (10 checks, ca. 1 hr after the dark period began; 7, 2 hr; 5, 3 hr; 3, 4 hr; 3, 5 hr; 3, 7 hr; 3, 9 hr; 3, 10 hr; 10, 11 hr). The spiders were copulating during 36 of the 47 checks. Another 16 pairs were observed continuously under red light for 3 to 6 hr, and 4 were observed continuously the entire night. These 20 pairs copulated during $85.6 \pm 17.20\%$ of the observation period.

For pairs not observed continuously, estimates of copulation durations never more than doubled the recorded copulation durations (observed portion of copulation/observed + estimated portion: $65.4 \pm 8.50\%$; range, 50.5% - 95.0%; n = 89).

Since data related to copulation duration were not normally distributed, means and ranges, but not standard deviations, will be provided. Each time that estimated copulation

durations were involved, Mann-Whitney U-tests were performed twice, once using estimated values and once excluding the estimated portions of each copulation. The two tests gave consistent results each time.

Type of Female and Her Location.—Copulations during which females were outside their nests tended to be shorter (Fig. 3) than when females were inside nests, the longest usually involving those females that had been cohabiting since the subadult stage (Fig. 4 and 5). Each of the three groups was significantly different from each of the other two (Table 1, rows 1-3; $P < 0.001$).

The longest copulation observed outside a nest began in the early afternoon and ended the following morning. My intermittent observations suggested that the pair copulated continually the entire night. If so, this meant that the copulation lasted 17.97 hr. All other copulations outside nests were observed continuously. None of these took place during the night, and none were nearly as long in duration as this one. The next longest copulations were 152 min, 70 min, and 68 min. All others lasted 31 min or less, usually much less. Why one copulation extended into the night and had an exceptionally long duration is not known.

During most copulations outside nests, the spiders were in essentially bare cages. The 18-hr copulation indicated that lengthy copulations are possible outside nests, raising the question of whether they might be more common under natural conditions in which vegetation, rocks, and other shelter are available. This hypothesis was investigated by observing spiders in field cages and terraria containing vegetation (see Jackson 1977a). All females for these observations were virgins. There was no indication that the presence of rocks and vegetation prolonged copulation (Table 1, compare rows 4 and 5). Also, the spiders copulated wherever they met, showing no tendency to go under shelter. Data for the field cages and terraria, being similar, were pooled.

Reluctance of Female to Depart Nest.—When mating occurred outside nests, bouts of not copulating interspersed within bouts of copulating were shorter and less frequent than when mating took place inside nests (Jackson 1977a). Typically during these

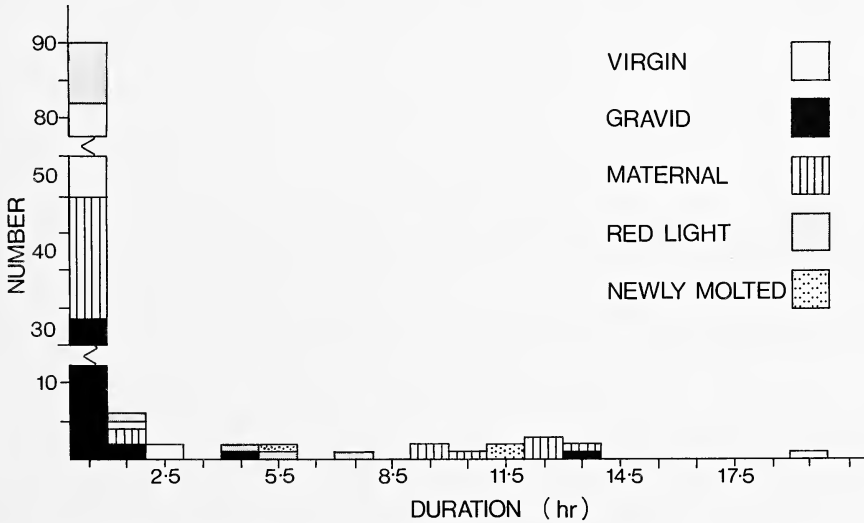


Fig. 4.—Durations of copulations. Female inside nest when encountered by male. Types of females (virgin, gravid, etc.) defined in text. "Virgin" does not include "newly molted" and "red light." 0.5: 0-59 min; 1.5: 60-119 min; 2.5: 120-179 min; etc.

periods, the male repeatedly mounted and stroked the female; but since her abdomen did not rotate, copulation could not take place. Periods of pausing, grooming, or other apparently non-reproductive activities, which sometimes occurred during these periods when the spiders were inside nests, almost never occurred when they were outside.

The minimum number of precopulatory mounts (ones which occurred previous to the male's last palp application) was 1, and any beyond this were interpreted as successful attempts by the male to continue copulation. The mean number of precopulatory mounts when the pairs met outside nests was 1.22, and the maximum was 7. (Observations on the 18-hr copulation were excluded from the calculations here since it was not watched continuously; however, only one mount was observed for this pair.)

The exact number of precopulatory mounts was recorded for 111 pairs that mated inside nests without cohabiting (mean, 2.41; max., 19). More than one precopulatory mount occurred during 49 of these copulations. In contrast, more than one precopulatory mount occurred for only 25 of the 191 pairs that mated outside nests ($\chi^2 = 36.80$, $P < 0.001$).

The number of precopulatory mounts for pairs mating after cohabitation was comparatively enormous. Based on a sample of 39 pairs, the mean was 27.56 and the maximum was 176. These values were probably gross underestimates since most of these copulations were not observed continuously. In each of these copulations more than one precopulatory mount was observed, compared to only 49 of 111 copulations of non-cohabiting pairs inside nests ($\chi^2 = 34.86$, $P < 0.001$).

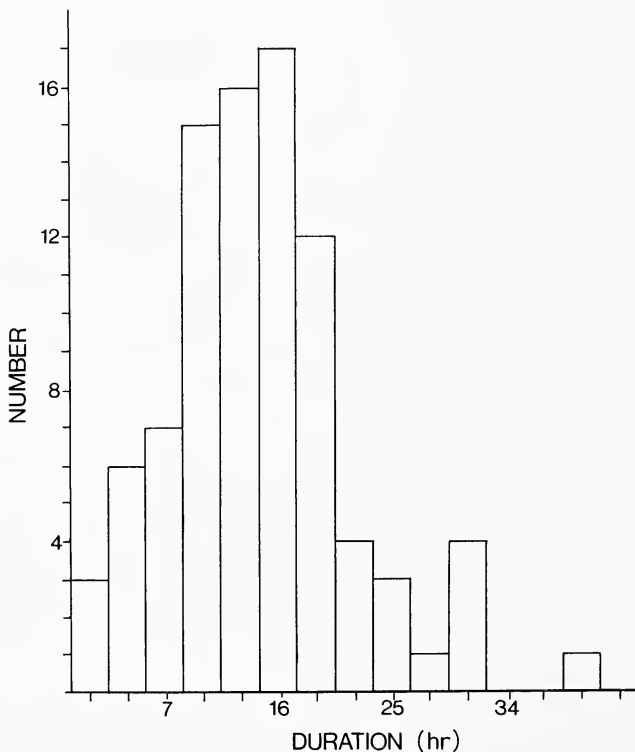


Fig. 5.—Durations of copulations preceded by cohabitation. 1: 0-179 min; 4: 180-359 min; 7: 360-533 min; etc.

These observations suggest a factor that might help explain why copulations tend to be longer when females are inside their nests. Apparently, the female's most effective tactic for terminating copulation is to decamp; but when she is inside her nest, decamping requires at least temporary departure from the nest. Females seem reluctant to depart their nests, and this is most likely related to the value of the nest in protection from predators, as a site for oviposition, etc. The trend in behavior of the female might be the result of an evolutionary compromise in which the advantages of terminating copulation by decamping are weighed against the disadvantages. If the female is outside her nest already, the disadvantages would seem relatively small; and we would predict these females would decamp more readily.

Spiders in individual laboratory cages generally remained in their nests one or more days after molting, and spiders in nature seem to be similar in this respect (Jackson 1979). Perhaps physiological processes, such as cuticle hardening, are optimally carried out inside nests during this period. Whatever the reasons, however, reluctance to depart the nest immediately following molting may account for relatively long copulations following cohabitation. Observations on 3 females that did not cohabit are of interest in relation to this hypothesis. A male was introduced into the cage of each female 1-2 hr after she molted, and each pair mated inside the nest. These copulations lasted 6.05 hr, 11.52 hr, and 11.73 hr. In the case of all other virgin females for which copulation was not preceded by cohabitation, molting occurred at least one day previous to introduction of the male, and copulation duration tended to be shorter (Fig. 4; Table 1, rows 6 and 7; Mann-Whitney U-test, $P < 0.01$).

Phidippus johnsoni almost always remains inside a nest at night, which is not surprising for a vision-dominated, diurnal animal. In a study comparing the sensory modalities employed in types 1 and 2 courtship (Jackson 1977b), females mated inside nests under dim red light, and one would expect these females to be hesitant to depart their nests. It is of interest that these copulations were relatively lengthy when compared with ones that began under regular light (Fig. 4; Table 1, rows 6 and 7; Mann-Whitney U-test, $P < 0.05$).

Female *P. johnsoni* tend to remain in their nests with their eggs, possibly protecting them from parasites and predators; and sometimes they oviposit several successive batches in a single nest (Jackson 1979). One might expect maternal females to be especially reluctant to depart their nests. In the laboratory, females occupying nests with their eggs copulated longer than the largest class of non-maternal females inside nests (virgins, regular light: Fig. 4; Table 1, rows 6 and 8). Since the difference approached but did not reach significance (Mann-Whitney, $0.05 < P < 0.10$), this factor should be investigated further.

IV. RELATIONSHIP BETWEEN COPULATION DURATION AND FERTILITY

Introduction and Methods.—One might expect more sperm to be transferred during longer copulations, resulting in a positive correlation between copulation duration and the number of fertile eggs oviposited by the female. This hypothesis will be considered next.

Virgin males and females (collected as subadults) were assigned to two groups. Each female in the long-copulation group mated on the day she molted after cohabiting with the male (copulation duration: 5-24 hr). Each female in the short-copulation group mated outside the nest within 2 days after molting (copulation duration: 2-8 min, except for one pair which copulated for 29 min). Each male underwent his final molt 5-25 days

previous to copulation, and there was no evidence that the fertility of females was influenced by the age of the males with which they mated. The number of fertile egg batches oviposited was recorded; and for each fertile batch, a record was kept of the number of spiderlings that emerged and the number of eggs that failed to hatch. (For information on oviposition and hatching of eggs, see Jackson 1978b.)

Results and Discussion.—Copulation apparently had an all-or-none, non-graded effect on fertility. Some copulations did not produce fertile eggs. However, if one considers only the fertile matings, there was no relation between how many fertile eggs a female oviposited and whether the copulation lasted a few minutes or several hours. Females in the long-copulation group produced 172.4 ± 46.14 fertile eggs, compared to 192.8 ± 94.92 for the short-copulation group (Table 2). The total number of fertile batches was 3.36 ± 1.29 for the long-copulation group, compared with 3.20 ± 1.30 for the short-copulation group. The long-copulation group produced 71.3 ± 12.45 ($n = 11$) fertile eggs in the first batch, 60.6 ± 12.49 ($n = 10$) in the second batch, and 45.6 ± 13.27 ($n = 9$) in the third. The comparable data for the short-copulation group are 74.4 ± 22.95 ($n = 5$), 63.5 ± 12.71 ($n = 4$) and 49.3 ± 13.52 ($n = 4$).

The all-or-none relationship probably holds for even the shortest copulations. In other studies, females were provided opportunity to mate repeatedly (see Section V). When we consider only the females that copulated only once, despite repeated opportunities, one oviposited fertile eggs after a copulation which included only one palp application lasting 1 min. She oviposited 139 fertile eggs in 2 batches. Although other females oviposited fertile eggs after single copulations of 2-3 min, their eggs were not counted.

There was a consistent trend with respect to whether matings were fertile or not. Each of the 11 females in the long-copulation group, but only 5 of the 10 females in the short-copulation group, oviposited fertile eggs ($\chi^2 = 4.726$, $P < 0.05$).

Data were available for another 66 females that copulated a single time before ovipositing. Although their eggs were not counted, each was maintained in the laboratory sufficiently long to oviposit at least one batch of eggs (see Jackson 1978b). Of these, 26 copulated 30 min or less; and 40 copulated 5 hr or more. Data from these females were added to the data from the 21 previously discussed females. A total of 19 females were infertile after short copulations; 17 were fertile. In the long-copulation group, all 51 females were fertile ($G = 53.578$, $P < 0.005$).

V. RELATIONSHIP BETWEEN COPULATION DURATION AND FIDELITY

Introduction.—Although there are numerous exceptions, the general trend among animal species seems to be that males attempt to copulate with many females, whereas females are more discriminating and mate with relatively few males (Bateman 1948). Although this trend probably occurs in spiders, it has not been investigated thoroughly. There are frequent references in the literature concerning males of spiders mating with more than one female. Female spiders are more often, but not always, reported to mate with a single male; however, reports from different researchers on the same species are not always consistent. In *P. johnsoni*, the difference between virgin and non-virgin females was not so simple. Sometimes non-virgin females re-mated, but compared to virgin females they mated less readily.

The probability that a previously mated female will copulate with a second male should be the product of two factors, the frequency with which she encounters courting males and her fidelity to the first male (i.e. whether she refuses to mate again when another male courts her). The relation between fidelity and the duration of the female's first copulation will be considered in this section.

Table 2.—Relationship between copulation duration and oviposition.

Spider	Duration of copulations (min.)	Number of fertile batches	Number of fertile eggs
1	4	4	295
2	6	1	64
3	6	3	180
4	7	4	149
5	8	4	276
6	300	2	158
7	300	4	179
8	480	3	161
9	600	5	213
10	660	3	238
11	840	4	180
12	900	5	189
13	1020	4	195
14	1140	1	67
15	1440	2	122
16	1440	4	194

Terminology.—A *virgin* female is one that has not copulated. A female that has copulated is *non-virgin*, regardless of whether she has been inseminated, a distinction that will be clarified later.

A *second-day* female is one which completed her first copulation 24-48 hr previous to the time of the test in question.

Typically a female feeds voraciously after copulating for the first time. A week or two later, her abdomen is distended, having a width noticeably greater than that of the cephalothorax. These females are defined as *gravid*. Only those gravid females that had not yet oviposited for the first time were considered in this study.

A *maternal* female is one which has recently oviposited fertile eggs.

Methods.—A “test” occurred when a male was placed in the same cage with an adult or subadult female. “Successful tests” were cases in which courtship occurred. Unsuccessful tests were rare. A few successful tests ended when cannibalism occurred. Tests without cannibalism ended when the male became unresponsive to the female, either before or after copulation. An “unresponsive male” was one that neither courted, followed, nor watched the female. When a nest was present, the male was not judged unresponsive until he was no longer in physical contact with a nest containing a female (Jackson 1977a).

All tests were started in the morning or early afternoon. Sometimes a single male was employed in more than one test on a single day, but at least 60 min elapsed between successive tests involving the same male. A male was never tested more than once with the same female on the same day, although he might be randomly selected for testing with the same female on a different day. Once a male copulated, he was not used in further tests on the same day.

In a “test sequence,” a female was tested with successive males until she mated or until she had been tested with 4 males, whichever occurred first. A female that mated was defined as “receptive.” At least 4 min elapsed between tests in a sequence, usually much more. When a sequence was not completed in one day, it was continued the next day. In the case of females tested in nests, testing was postponed if they departed their nests prior to completion of a sequence. Testing continued on the same day if a female

returned to her nest before late afternoon. Otherwise, testing continued the following morning, since spiders almost invariably occupied nests just after the lights came on in the laboratory (Jackson 1979).

When a female was tested outside a nest, all nests in her cage were destroyed before the first male was introduced. Except for maternal females, females tested outside nests always departed their nests spontaneously prior to nest destruction. Maternal females were forced from their nests with a camel hair brush. When females were tested inside nests, any additional nests in the cages besides the ones being occupied by the females were destroyed prior to introduction of the male.

After a female copulated, whether she was fertile was defined by whether she oviposited fertile eggs. When females died without ovipositing less than 1 month after copulation, no judgment was made as to their fertility.

Each female was subjected to a test sequence on the second day, again when she was gravid, and also when she was maternal. All second-day and gravid females, except those in Set B (see below), were tested outside nests only. Test sequences with gravid females always began at least one week after the sequences on the female's second day. From among the females that were unreceptive when gravid, each of 18 were subjected to another test sequence, outside nests while still gravid, one week after the previous sequence.

After I determined that the female's first batch of eggs was fertile, she was subjected to 2 test sequences after later fertile ovipositions. One of these was with the maternal female inside her nest with her eggs; the other was after a different oviposition, with the female outside her nest. Approximately half the females were first tested inside nests; the other half were first tested outside nests. Test sequences were carried out 2 to 7 days after oviposition. For inside-nest test sequences, the females occupied their nests with their eggs. For outside-nest test sequences, the females were forced from the nests and transferred to clean cages, and the test sequence was carried out ca. 24 hr later in a cage without nests. Eggs of maternal females were kept in glass vials long enough to ascertain their fertility.

Females in Set B were subjected to an abbreviated testing procedure, including test sequences on the second day and while gravid, but not while maternal. The gravid females in this set were tested inside nests.

For various reasons, it was not always possible to carry out all tests for all females. For example, sometimes after one maternal test sequence, the female died, escaped, or failed to oviposit again. All spiders used in this study were collected as immatures in nature, except that some females collected as adults were used as supplementary females in the maternal test sequences. When the supplementary females were collected with fertile eggs, test sequences began after they oviposited their first batch in the laboratory. Ones collected without eggs were not used until after they had oviposited an intervening batch of fertile eggs in the laboratory.

Results and Discussion.—For each reproductive state, both inside and outside nests, there were some females that copulated. Females which copulated for a relatively short time at their first mating were more likely to copulate again on the second day. Looking at this phenomenon in a slightly different way, females that were receptive on the second day copulated for a mean of only 94 min at their first mating, compared to a mean of 571 min for ones that were unreceptive on the second day (Fig. 6; Table 1, rows 9 and 10; Mann-Whitney U-test, $P < 0.001$). Similarly, the first copulation was longer for females that showed fidelity to the first male after tests on both their second day and

while gravid (Fig. 7; Table 1, rows 11 and 12; Mann-Whitney U-test, $P < 0.001$), and for those that showed fidelity during tests on their second day, while gravid, and while maternal (Fig. 8; Table 1, rows 13 and 14; Mann-Whitney U-test, $P < 0.01$). There was no evidence of short term fluctuations in receptivity since the 18 unreceptive gravid females that were tested again a week later remained unreceptive.

A problem in interpreting these data arises. Both copulation duration and pursuit time (Jackson 1979) tended to be much greater for spiders mating inside nests (not preceded by cohabitation) compared to those mating outside, and both tended to be greater still if cohabitation was involved. Possibly, the important factor influencing female fidelity was either pursuit time or simply to which of the three categories the copulation belonged (i.e., outside nest, inside nest without cohabitation, or inside nest with cohabitation). Attempts to ascertain statistically which of these factors was more important, using subsets of the existing data, were inconclusive. However, certain observations gave the impression that the important variable was indeed copulation duration.

Six females that cohabited before mating the first time were receptive on the second day; 63 were not. Two of the receptive females were ones that initially copulated, for unknown reasons, for unusually short periods, 6 min and 85 min. (Each of the other four females copulated 9 hr or longer.) Pursuit time, however, was not unusually short for any of these females (6.2 ± 1.83 days; min., 4 days). Among the females that did not cohabit, 3 initially copulated for ca. 6 hr or longer; all others copulated initially for ca. 2 hr or less. Two of these (copulation durations: 531 min, 351 min) were not receptive on the second day, despite the pursuit times preceding their first copulations being short (8 min

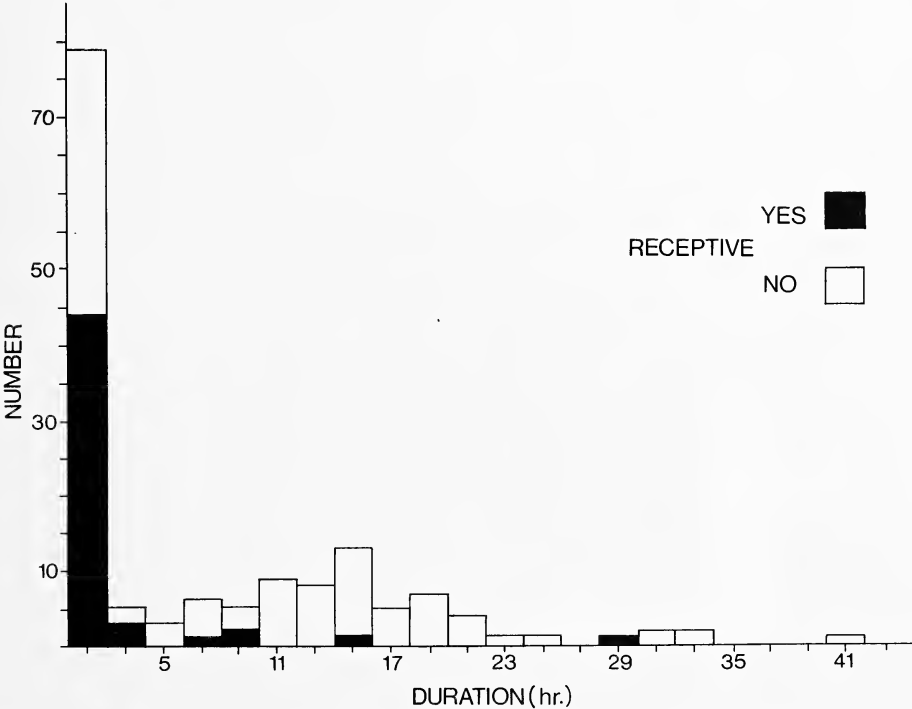


Fig. 6.—Number of copulations of differing durations. First copulation in life of each female. Females tested on second day (see text). Receptive: mated during the test sequence. Unreceptive: failed to mate. 1: 0-119 min; 3: 120-239 min; 5: 240-359 min; etc.

for both). (The other female, receptive on the second day; initial copulation, 378 min; initial pursuit time, 20 min.)

The nest was another factor that seemed to influence receptivity. Females inside nests were more likely to be receptive than females outside. Of the 54 maternal females tested both inside and outside nests, only 7 were receptive while outside nests, compared to 22 that were receptive while inside nests (McNemar test, $\chi^2 = 9.391$, $P < 0.001$).

In the case of gravid females, the same females were not tested both inside and outside nests. All those tested inside nests while gravid were ones that copulated 20 min or less at their first mating. Of those females tested outside nests while gravid, 77 copulated more than 20 min at their first mating, and these were deleted when the two groups were compared. Only 13 of the remaining 57 females were receptive when tested gravid outside nests. On the other hand, 24 of the 34 females tested inside nests were receptive ($\chi^2 = 18.220$, $P < 0.001$).

Reluctance of females to depart their nests, a factor discussed earlier with respect to pursuit time (Jackson 1978a) and copulation duration (Section III), may also influence receptivity. Gravid females seem less agile than other females, and this may increase their susceptibility to predators while outside nests. Besides, gravid females inside nests are likely preparing to oviposit, and this may contribute to their reluctance to depart nests. The reluctance of maternal females to leave their nests and eggs has been discussed previously.

To summarize, females of *P. johnsoni* may mate with more than one male. However, the trend seems to be that a female is more likely to mate again if her previous copulation was relatively short. This suggests a selection pressure favoring males with prolonged copulation: males that copulate for relatively long periods may tend to leave their sperm with females that are less likely to mate with other males. To evaluate this hypothesis properly, we need to know the relative frequencies with which females encounter additional courting males after copulations of differing durations. If females behave in such a way as to be equally or less likely to encounter additional males after relatively long copulations, then the proposed hypothesis seems probable.

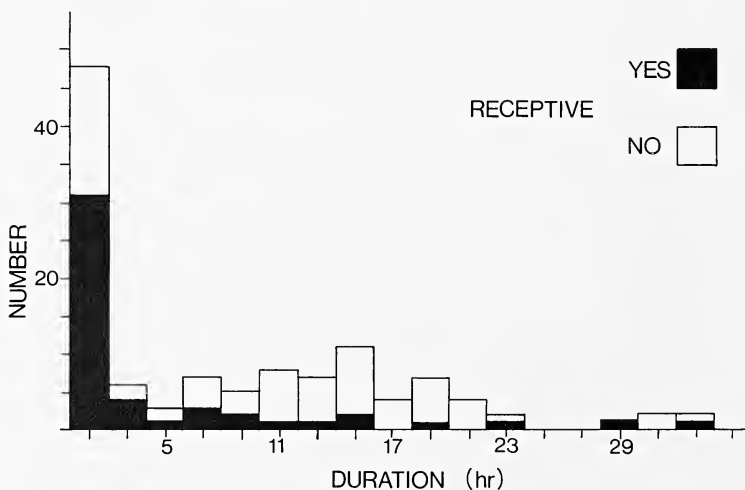


Fig. 7.—Number of copulations of differing durations. First copulation in life of each female. Each female tested on second day and when gravid. Receptive: mated during at least one test. Unreceptive: failed to mate during all tests. 1: 0-119 min; 3: 120-239 min; 5: 240-359 min; etc.

VI. INTERVAL BETWEEN COPULATION AND THE TERMINATION OF FEMALE RECEPTIVITY

Introduction.—After copulation, females of the mosquito *Aedes aegypti* become unreceptive to additional males; however, there is an interval of several hours between insemination and the termination of female receptivity (Craig 1967). It seemed important to determine whether a latency of this sort occurs in *P. johnsoni*. For a species in which there is a latency between insemination and the onset of female unreceptivity, natural selection might favor males that prolong copulation until the end of the latency period. Sperm competition would be reduced as a result of monopoly of the female by the male during the period when additional males might displace his sperm. I designed an experiment to investigate this in *P. johnsoni*.

Methods.—Twenty virgin females each copulated for 35 min or less. For Group A (10 females), a test sequence was begun immediately after the end of the first copulation and completed within 1 hr. Each female in Group B was subjected to a test sequence 8 to 9 hr after the end of the first copulation. All females were subjected to yet another test sequence ca. 24 hr after the initial copulation in order to ascertain the consistency of fidelity over this period. All test sequences were carried out with the females outside nests. All spiders were collected as subadults.

Results and Discussion.—Five of the 10 females in Group A copulated with a second male when tested within 1 hr of the initial copulation. Virtually the same proportion of females in Group B (6 of 10) copulated with a second male when tested 8 to 9 hr after the initial copulation. Only three females changed their state of receptivity when tested the second day.

Earlier (Section V) it was shown that 53% of 38 females that initially copulated outside nests were receptive on the second day, consistent with the results in this study

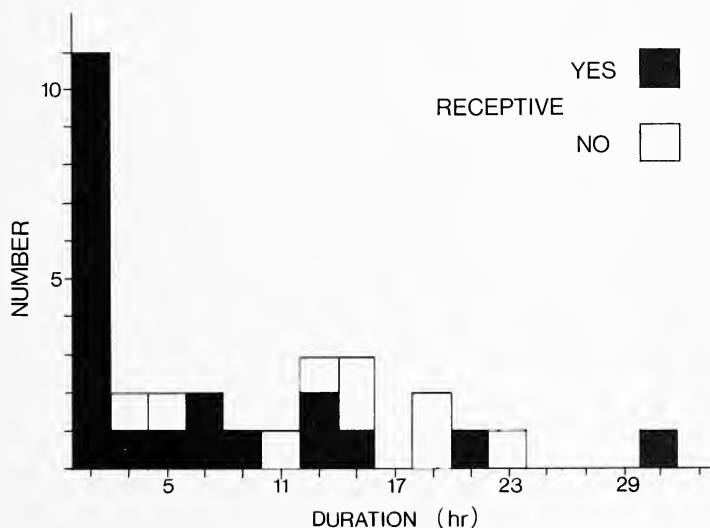


Fig. 8.—Number of copulations of differing durations. First copulation in life of each female. Each female tested on second day, when gravid, and when maternal, inside and outside nest (see text). Receptive: mated during at least one test. Unreceptive: failed to mate during all tests. 1: 0-119 min; 3: 120-239 min; 5: 240-359 min; etc.

for females tested within 1 hr, between 8 and 9 hr after, and ca. 24 hr after their initial copulation. Apparently, if the female becomes unreceptive after mating, the effect is virtually immediate.

VII. MATING PLUGS

Introduction.—After mating, the copulatory orifices of the females of *P. johnsoni* were frequently covered by a white, yellow, orange, or red substance which I referred to as the “mating plug.” (These never covered the orifices of virgin females.) No two plugs were exactly alike in size, shape, color, and texture. One or, more often, both orifices on the epigynum were covered. Gonopores were never covered. The material of the plug was sometimes concentrated over the orifices with the area between more sparsely covered. Sometimes the area between was completely uncovered, and the plug consisted of 2 discrete units. Other times, the plug was a large mass covering both orifices with no conspicuous differentiation into 2 parts. Asymmetries were common, with more material over one of the 2 orifices. Plugs varied from a fine film to a bulky mass. Usually they had a grainy appearance, but some were smooth and shiny. In some cases, plugs assumed the shape of wedges within the orifices. More often, they were highly sculptured, amorphous masses of material. A single plug could have components of varied color, texture, size, and shape (Fig. 9).

Mating plugs have been reported for other groups of spiders, including some Clubionidae, Oxyopidae, Thomisidae, Toxopidae, and Theridiidae (Brady 1964, Exline and Whitcomb 1965, Forster 1967, Muniappan and Chada 1970, Whitcomb and Eason 1965). In some araneid, oxyopid, and theridiid spiders, parts of the male's palpal organ are found embedded as plugs in the copulatory orifices of the female after mating (Abalos and Baez 1963, Bhatnagar and Rempel 1962, Brady 1964, Kaston 1970, Levi 1969, Robinson and Robinson 1978).

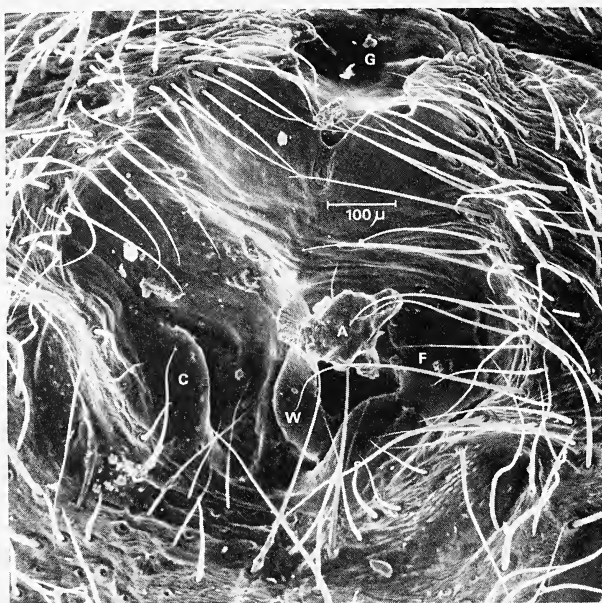


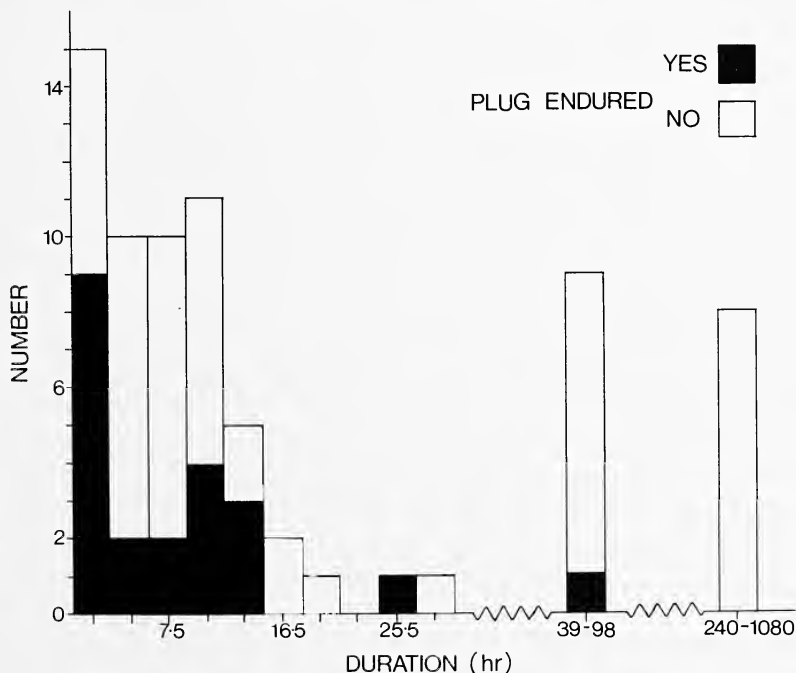
Fig. 9.—Epigynum (S.E.M.) of *Phidippus johnsoni*. C: copulatory orifice. Plug, over one copulatory orifice, in 3 forms (A: amorphous mass, F: film, W: wedge situated in orifice). G: gonopore.

Functions of plugs related to reduction of sperm leakage and to sperm competition (hindrance of insemination by additional males) both might be involved (see Parker 1970); the latter will be considered here for the plugs of *P. johnsoni*.

Methods.—Concurrently with the study of fidelity (Section V), females were checked for plugs. Checks were made within 12 hr after virgin females copulated and within 24 hr after later copulations. Females in Set B were not checked. Dry ice, which produces low temperatures and carbon dioxide gas, was used to anesthetize the spiders for 1-2 min while they were examined under a microscope.

Whenever a plug was present, it was described and a sketch was made. Evidently, plugs did not change in appearance spontaneously. A second examination of 24 females occurred when they died 2-5 mo after their last copulations. Another 20 females that were not involved in the study of fidelity were examined within 24 hr after their first copulation and again 2 weeks later, without having mated again. Of these 44 females, 24 had plugs at the later examinations that matched the descriptions of their previous plugs; the other 20 lacked plugs at both examinations.

Results and Discussion.—On 74 occasions males copulated with females that already had plugs from previous copulations. Afterwards, either a different plug or no plug was present in 52 cases. In the other 22 cases the previous plug was still present, indicating that it had protected the previous male's sperm investment; and in 2 of these cases a plug endured 2 subsequent copulations. These data suggest that plugs are effective ca. 30% of the time. However, since only the exteriors of genitalia were examined, a substantial part of the plug might not have been visible; and 30% effectiveness might be an underestimate. Another consideration is that a male may sometimes alter the previous male's plug, possibly add a plug of his own, but fail to inseminate the female.



Considering females initially lacking plugs, both virgins and non-virgins, there was no evident relation between whether a plug formed and copulation duration (Table 1, rows 15 and 16). However, the possibility of internal plugs must be kept in mind.

There was also no evident relation between the duration of the copulation just previous to formation of the plug and whether the plug endured succeeding copulations (Table 1, rows 17 and 18), but there was a relation between plug endurance and the succeeding copulation. Considering copulations involving females already possessing plugs, copulations after which the previously present plug endured tended to be much shorter than those after which plugs did not endure (Fig. 10; Table 1, rows 19 and 20; Mann-Whitney U-test, $P < 0.01$).

In conclusion, plugs seem to be adaptations related to sperm competition in *P. johnsoni*. If a male leaves a plug on the female's copulatory orifices after mating, then his sperm investment is protected to some extent even if the female is receptive to additional males. The plug forms a physical barrier that a second male must overcome before he can copulate with the female and displace the first male's sperm. This probably requires a variable but substantial proportion of the duration of the second male's copulation. One can manually push plugs off the genitalia of anesthetized females by using an insect pin. Perhaps the male physically displaces the plug in a similar way using structures on his palp. This suggests that when plugs endured second copulations, females tolerated the presence of males for a time insufficient for them to displace plugs left by earlier males. When males mate with non-virgin females, the time required to displace plugs may be one of the factors favoring males that copulate for prolonged periods.

VIII. RELATIONSHIP BETWEEN FERTILITY AND FIDELITY

Introduction.—As shown in the study of female fertility (Section IV), all females did not oviposit fertile eggs after a short copulation. In the study of female fidelity (Section V), it was shown that females were more likely to be receptive after a short copulation than after a long one. These two observations suggested the hypothesis that the mated females which were receptive were ones that could not oviposit fertile eggs from the previous copulation alone.

Methods.—Each of 18 virgin females copulated 16 min or less. Within 12 hr afterwards, their copulatory orifices were covered by Eastman 910 Adhesive (Tennessee Eastman Co., Kingsport, Tennessee). These females will be referred to as "cemented." Cemented females were not prevented from ovipositing since their gonopores were not covered, but they could not be inseminated again. When they oviposited, any sperm that fertilized their eggs came from the first copulation even if they had been receptive to additional males. There were 10 "control females." Each was cemented when still virgin and permitted to "mate" the following day.

With the anesthetized spider inverted under a microscope, her copulatory orifices lay in a basin at the anterior end of her epigynum. The adhesive was taken into a microcap (Drummond Scientific Co.). When the microcap was brought briefly into contact with the anterior epigynum, a drop of adhesive filled the basin and covered the copulatory orifices. Using an insect pin, I spread the adhesive evenly in the basin, and pressed the long setae near the anterior of the epigynum into the adhesive. The spider was kept under anesthesia for an additional 5 min while the adhesive dried. Any plugs present on the epigynum were rapidly dissolved by the adhesive.

Results and Discussion.—Apparently, the adhesive effectively prevented insemination. Each control female lived well beyond the normal preoviposition period, and none oviposited fertile eggs. "Copulatory behavior" of males with cemented females was not greatly different from normal. Sometimes they scraped their palps on the epigynum for relatively prolonged periods, but each eventually held his palp stationary against the epigynum, with the hematodocha pulsating.

Eleven mated cemented females were receptive to additional males; 7 were not. Five of the receptive ones oviposited fertile eggs, indicating that receptive females included ones with fertile sperm from previous copulations. This was not consistent with my original hypothesis.

A related hypothesis can be considered. Although fertile females may be either receptive or unreceptive, one might expect all infertile females to be receptive. However, 2 of the infertile females were unreceptive. One might expect that at least a greater proportion would be receptive than unreceptive, but there was no indication of this either (G-test of independence, n.s.).

Another consideration is that although some fertile females were receptive, perhaps they carried fewer stored sperm compared to unreceptive fertile females. However, this hypothesis is not supported by available data either. The 5 fertile receptive females oviposited a mean of 119 ± 32.1 fertile eggs. The 5 fertile unreceptive females oviposited a mean of 145 ± 52.1 fertile eggs (t-test, n.s.). Evidently female receptivity is not simply related to an insufficient quantity of stored sperm.

IX. CONSEQUENCES OF REPEATED COPULATION

Introduction and Methods.—After copulating with one male, a female may be fertile and yet copulate with another male (Section VIII), creating conditions for sperm competition. The loss suffered by the first male should be a product of the probability that the female will mate with other males and the consequences of any additional matings that occur. The probability of repeated mating was discussed in Section V. This section will be concerned with the consequences; i.e., the proportion of the female's eggs fertilized by each male. The sterile male technique has been frequently used in similar studies with insects (Parker 1970). The female mates with two males, one with sterile and one with fertile sperm. Sterility can be induced by hybridization, chemosterilants, or irradiation. Eggs which hatch are attributable to the fertile male. A certain percentage of a female's eggs may normally fail to hatch after a copulation with a fertile male, but any increase beyond this percentage is attributable to the sterile male.

Using a Machlett X-Ray Machine (Picker X-Ray Corp., Cleveland, Ohio) with a beryllium window, two groups of adult male *P. johnsoni* were subjected to x-radiation (dose rate, 17.5 rads per sec): Group A, 10 krad; Group B, 30 krad. During irradiation, each spider was in an individual container (ca. 20 x 12 mm) made from 2-mm-thick plastic tubing, stoppered at each end with cotton. All spiders were irradiated on the same day.

Each irradiated male mated with two virgin females outside nests, the control and the experimental. Each control female mated with an irradiated male only, and her eggs were monitored to ascertain the male's sterility. Each experimental female mated first with an irradiated male and later with a normal male. Each group of irradiated males was divided into two subgroups. For one, mating took place on the second and third day after irradiation; for the other, on the ninth and tenth day. When gravid, each female was

subjected to test sequences (Section V) with normal males, until one of the two females corresponding to each irradiated male mated. The other female became the control.

Results and Discussion.—There was no indication that male longevity, health, or behavior was affected by irradiation. All control females were infertile, indicating that both 10 krad and 30 krad are sublethal sterilizing dosages for *P. johnsoni*, with effects that persist at least 19 days. Data from all groups and subgroups will be pooled for the following discussion.

That irradiation did not render males aspermic was confirmed by examining eggs of control females. Embryos formed from these eggs, but each died at an early stage of development. Irradiation probably caused dominant sublethal mutations in sperm, as generally occurs when this technique is used with insects (Smith and Borstel 1972).

The copulations of irradiated males were all short (19.0 ± 16.53 min; max., 76 min). Although females sometimes fail to oviposit fertile eggs after short copulations with fertile males (Section IV), it is extremely unlikely that this alone accounts for the infertility of the 29 control females.

Of the 22 experimental females, 12 were infertile. Apparently in these cases the second male was unsuccessful at displacing any of the first male's sperm. The females in this study were not examined for plugs, but it seems likely that some irradiated males left plugs which blocked the second males' attempts to inseminate the females.

Normally, after mating with a fertile male, the mean proportion of eggs which hatch decreases as the female oviposits successive batches (Jackson 1978b). In 6 cases the hatch proportions of experimental females in this study were similar to those for normal females for each batch they oviposited. Apparently the second male completely displaced the irradiated male's sperm in these cases.

The hatch proportions for the first batches of each of the remaining 4 females (0.0408, 0.1127, 0.6290, 0.6667) were compared individually with the first batch hatch proportions of normal females (0.89 ± 0.085): t-values were 9.351, 8.558, 2.451, and 2.866, respectively; $P < 0.05$ for each.

Apparently these were cases in which the second male's sperm only partially displaced that of the first male. The spiders in this study were not maintained long after their first batch. However, one oviposited a second batch, and the hatch proportion was similar to that for second batches of normal females. Studies designed to look at sperm utilization in later batches are needed.

To summarize, three different consequences were associated with a second male copulating with a previously mated female: failure to displace any of the first male's sperm (55% of the cases), partial displacement (18%), and total displacement (27%). Since larger sample sizes and reversal of the sequence of mating (females mating with normal males first; irradiated males second) might alter estimates of these frequencies, the qualitative conclusion will be emphasized. The male's losses through female infidelity are potentially large in *P. johnsoni*, since his sperm may be partially or totally displaced when the next male copulates. Males that reduce such losses by prolonging copulation should be favored by natural selection.

X. MECHANISMS CONTROLLING FEMALE RECEPTIVITY AND THEIR ADAPTIVE SIGNIFICANCE

Although the mechanisms by which copulation induces unreceptivity in *P. johnsoni* are unknown, studies of insects provide some suggestions. In some Diptera, sperm or

other substances ("matrone" or "accessory material") originating from the male reproductive tracts induce unreceptivity in females (Leopold 1976). In *Musca domestica* prolonged copulation is linked to mechanisms inducing female unreceptivity. Copulation generally lasts ca. 1 hr, yet virtually all sperm transfer occurs during the first 10 to 15 min (Murvosh *et al.* 1964). During the remaining time, transferral of accessory material takes place. Perhaps something similar occurs in *P. johnsoni*, although accessory substances have not yet been looked for in spiders. If the female's unreceptivity is positively correlated with the quantity of accessory material transferred, this might in turn be correlated with the duration of copulation. A quantitative effect of this sort would seem to be the case in *M. domestica* (Leopold *et al.* 1971, Riemann and Thorson 1969).

In some insects there is evidence that female unreceptivity is induced by mechanical stimuli concurrent with copulation (Obara *et al.* 1975, Truman and Riddiford 1974). It would be of interest to look for tactile receptors associated with the epigynum of *P. johnsoni*, and a relationship between the quantity of stimulation received and the probability that the female will be unreceptive. Such stimulation might act on the female's central nervous system by either a neural or endocrine pathway, both of which have been implicated in insects. However, since the onset of female unreceptivity is sometimes virtually instantaneous, a neural pathway seems more likely in *P. johnsoni*.

Often in insects one male at one copulation can completely fill the female's sperm storage capacity (Parker 1970), and this seems likely for *P. johnsoni* also. There is no indication in *P. johnsoni* that the number of fertile eggs oviposited is increased when the female copulates more than once. Also the male's sperm remains viable in the female's spermathecae for many months. Mating might expose females to increased predation risks (Jackson 1976). Time involved in supernumerary copulations might be optimally used for other activities, such as feeding, nest building, etc. Considering these factors alone, one would predict natural selection to favor females that become unreceptive after a single insemination. This raises questions concerning the ultimate causes of mechanisms by which female fidelity is linked with copulation duration.

In a variable or unpredictable environment, it may be that the females that increase the variance of their progeny by copulating with more than one male might have a selective advantage over females that mate with only one male (Williams 1975). Because of three considerations, this hypothesis seems inadequate for *P. johnsoni*. Although repeated mating occurs, it seems relatively infrequent; and when it occurs, sperm mixing is not the rule. However, the main difficulty is that this hypothesis provides no apparent explanation for the linkage of fidelity and copulation duration.

If the female's tactics for ridding herself of a persistent male are relatively ineffective, she may run greater risks of predation and waste more time by resisting rather than by copulating. This factor, which can be considered as a form of rape (Parker 1974), was discussed earlier in reference to the relatively great receptivity and copulation duration of females occupying nests. Rape in the more literal sense of copulation with continually resisting females apparently does not occur in *P. johnsoni*. The difficulty with this hypothesis, as with the previous, is that it provides no apparent explanation for the linkage of fidelity and copulation duration at the previous mating.

Short copulations are apparently more likely to be infertile. Suppose the female cannot detect the presence of sperm. This might lead to selection pressure favoring females that are less likely to show fidelity to a male after a short rather than a long copulation. By mating again these females may significantly increase the chances that they will be fertile.

In many habitats, other *Phidippus* species occur sympatrically with *P. johnsoni*, and reproductive isolation is another factor that might be important in relation to female fidelity. Relatively long copulations might be less likely with heterospecific males. Copulation itself might not persist long if the male is of a different species; and a less direct, but perhaps more important, consideration may be that longer copulations tend to be associated with longer precopulatory associations. During the relatively long courtships when females occupy nests and especially during the very long associations when pairs cohabit, there may be a significantly greater probability that heterospecific pairs will fail to copulate because the female and/or the male make species discriminations. (For similar arguments concerning birds, see Mayr 1970). Although the duration of the precopulatory association might be of greater relevance than copulation duration, copulation duration might be more readily measured by the female.

XI. CONCLUSION

It is often tempting to envisage the courtship of animals as variable among species but essentially uniform within species. This portrayal was found to be misleading for the courtship of *P. johnsoni* (Jackson 1977a). The courtship of this species encompasses many elements of behavior, some of which occur only rarely; and the sequence in which they occur during interactions varies greatly. In addition to complexity of this type, precopulatory behavior is organized into two distinct types of courtship and three alternative mating tactics.

Copulatory behavior is also complex in *P. johnsoni*; and as with precopulatory behavior, consideration of the alternative mating tactics is crucial in understanding variation in copulatory behavior. For example, there is no simple answer to questions concerning the typical duration of copulation in this species. Copulation duration in *P. johnsoni* varies over almost the entire range known for the animal kingdom, but there is a trend related to mating tactics: copulation is short with females outside nests, longer with females inside nests, and very long after cohabitation.

Variation in copulatory behavior highlights another question that is frequently viewed as misleadingly simple, namely the function of copulation. Certainly, transfer of sperm as a preliminary to fertilization is a major function, but the present study has illustrated the need to consider sperm competition and other functions.

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THE MATING STRATEGY OF *PHIDIPPUS JOHNSONI* (ARANEAE, SALTICIDAE): III. INTERMALE AGGRESSION AND A COST-BENEFIT ANALYSIS

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ABSTRACT

Similarities between the mating strategy of the males of *Phidippus johnsoni* and models for optimal foraging are discussed. A predator encounters potential prey, each of which has an associated search time (S_i) and pursuit time (P_i) per net benefit. In principle, net benefit (benefits minus costs or risks) should be expressed in units of fitness. Males of *P. johnsoni* encounter females differing in location and maturity, each of which has an associated S_i and P_i . The numerators of P_i vary in the following order: adult female outside nest (ca. 2 min), adult inside nest (16 min), subadult inside nest (1 week). Denominators seem to follow the opposite trend. Considering fertility, sperm competition, cannibalism, predation, and male-male aggressive interactions, net benefit for males seems to be least if they pursue adult females outside nests, greater if they pursue adults inside nests, and greatest if they pursue subadults inside nests. The optimal type of female, the type with the smallest P_i , is probably a subadult inside her nest.

INTRODUCTION

There are certain similarities between the mating strategy of a salticid spider, *Phidippus johnsoni*, and models for the evolution of predatory strategies. In these models, a predator encounters different types of prey with which it may use different predatory tactics, and each type of prey requires differing search (S_i) and pursuit (P_i) times per unit net benefit. Males of *P. johnsoni* encounter different types of females which they pursue with distinctly different tactics: (1) adult females outside nests, type 1 courtship (pursuit time, P_o) (2) adult females inside nests, type 2 courtship (P_n) (3) subadult females inside nests, cohabitation (P_s). In an earlier paper, only the numerators of P_o , P_n , and P_s were considered (Jackson 1978a). The denominators (net benefit) will be considered in this paper.

The benefit to the male from mating with a given female might be viewed as the number of progeny she will leave after copulation under conditions that are optimal for the male. Optimal conditions would include absence of other males that might copulate with the same female, etc. Using net instead of simple benefit as the denominator takes into account less than optimal conditions for the male.

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The benefit a male derives from a given copulation depends on the number of fertile eggs the female oviposits, the probability that she will not copulate with another male (fidelity), and the consequences of additional copulations if the female should mate again. Cost might be related to risks such as predation, cannibalism, and various types of physical interference. Data concerning these factors have been presented elsewhere (Jackson 1976a, b, 1980a). In this paper I will present data related to aggression, another potential factor affecting net benefit. This will be followed by a comparison of P_o , P_n , and P_s .

Aggression will be loosely defined as behavior directed toward causing physical harm to a conspecific individual (Hinde 1974). It is useful to exclude cannibalism from the definition in the present context.

Threat displays and ritualized fights were sometimes performed by all sex/age classes of *P. johnsoni*, but this type of behavior was most pronounced in adult males, occurring invariably when two males were placed together in the laboratory (Jackson 1977). If a male encounters another male that is courting or copulating with a female, the aggressive interaction which ensues either temporarily or permanently interrupts the first male's interaction with the female. I designed an experiment to compare the consequences of intermale interference when males pursued females inside and outside nests.

METHODS

Apparatus—Cages were the same as those used for recording cohabitation duration (Jackson 1978a) except that they had four instead of two entrances (Fig. 1). During maintenance, each entrance was plugged with a cork. During observations, plastic corridors were substituted for the corks in two of the entrances. Each corridor contained a narrow slit cut half-way through from the top. A stiff paper partition fit inside the slit, and it was shaped so as to fill the corridor and prevent passage by the spiders. During observations cages were connected by corridors to terraria, and each terrarium was filled with a meshwork of corrugated cardboard.

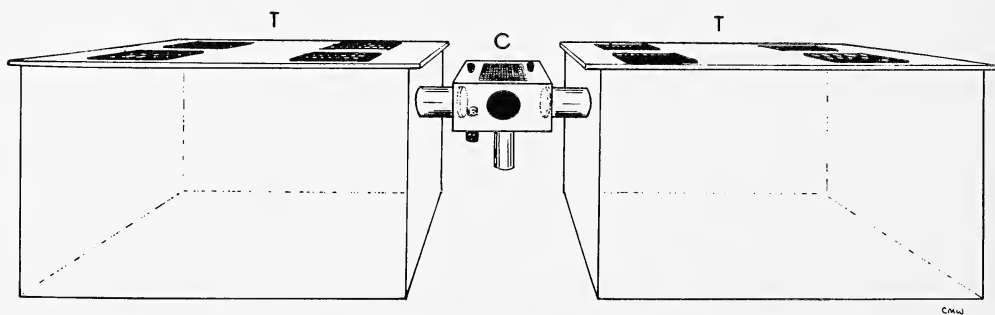


Fig. 1.—Apparatus for observing consequences of aggressive interactions (not to scale). C: Transparent plastic cage (10 x 10 x 6.5 cm) with 4 entrances (4.5-cm-diameter holes); 2 entrances plugged with corks (one shown: large blackened circle in front of diagram); 2 fitted with corridors (5-cm-long transparent tubes). Top of cage: two 1-cm-diameter holes plugged with corks (small black circles) and a 4.5-cm-diameter hole covered by metal screen for ventilation. Bottom of cage: glass vial containing sugar (food for flies) inserted through hole (1.5-cm-diameter, center of cage), moist cotton roll inserted through 1-cm-diameter hole (on left). T: Transparent plastic terrarium (56 x 53 x 30 cm). Lid (61 x 61 cm transparent plastic) with 4 holes covered by metal screen. Entrance on side accepts corridor from cage (top of entrance to lid: 5 cm). See text for details.

Table 1.—Consequences of intermale aggression in the presence of females. Each observation: one male (resident) courting or copulating with female when second male (intruder) begins interaction (intrusion). Females outside nests: Groups 1 and 2; inside: Groups 3 and 4. Intrusion while resident courted: Groups 1 and 3; copulated: Groups 2 and 4.

Group	Female Inside Nest	Resident Already Copulating	MALE WITH WHICH FEMALE MATED AFTER		
			INTRUSION		
			Resident	Intruder	Neither
1	No	No	0	0	12
2	No	Yes	2	0	10
3	Yes	No	1	8	3
4	Yes	Yes	3	2	7

Procedure— Except for specific differences noted here, maintenance and testing procedures were as described previously (Jackson 1978a, 1980b). Females were maintained individually in the cages for 1 to 2 weeks previous to testing. Each built at least one nest, always partially fastened to one of the large corks in the entrances. To begin a test, two entrances were fitted with corridors. When a nest was required for the test, the pair of entrances was chosen so as not to damage the nest occupied by the female; when not required, all were destroyed before the corridors were connected.

Virgin females were assigned to 4 groups (Table 1). To begin a test, first one male (“resident”) was introduced into the female’s cage through one of the small cork holes at the top of the cage. A second male (“intruder”) was introduced either while the first male copulated (Groups 2 and 4) or while he courted the virgin female (Groups 1 and 3). The female was either outside (Groups 1 and 2) or inside (Groups 3 and 4) the nest when the intruding male encountered the resident male-female pair. Using enamel paint, each male was marked with an identifying color combination (see Jackson 1979).

When the intruding male encountered the male-female pair, the partitions were removed from the corridors, providing the spiders with access to the terraria. Observation was continued until 15 min after the last interaction between any 2 of the spiders. The terraria provided space to which the spiders could escape from each other after interaction, and the corrugated cardboard increased surface area and provided shelters for hiding.

Statistical tests are from Sokal and Rohlf (1969). Data are given as means ± S.D.

RESULTS

When encountering another male that was courting a female, the intruding male began by courting the female (female outside nest, 4 cases; inside, 7) or by threatening the male (outside, 8; inside 5). Usually the resident males reciprocated almost immediately when the pair was outside the nest with threat displays. With the female inside her nest, the two males generally alternated between interacting with each other and courting the female from opposite ends of the nest.

The initial responses of males encountering mating pairs was to court. Sixteen (11 outside, 5 inside) mounted the mating pairs and walked, tapped, scraped, and stroked (postmount courtship; Jackson 1977) on both the female and the male; and in eight cases (5, outside; 3, inside) the males embraced and pushed each other while standing on the female.

Almost all females that were outside their nests (Groups 1 and 2) decamped and entered one of the terraria while the two males interacted. The exceptions were two cases in which the intruder mounted and the males embraced and pushed, after which the intruder decamped; and the resident male renewed copulation without having dismounted.

Considering cases in which intruding males encountered courting male-female pairs (Groups 1 and 3), copulation more frequently followed male-male interactions when females were initially inside rather than outside nests ($\chi^2 = 11.368$, $P < 0.001$). (When the male-female pairs were already copulating before the intrusions, these frequencies were not significantly different.)

When nests were present, all copulations except one transpired inside nests. The exception was a female in Group 4 that departed her nest after the intrusion. She remained in the cage and mated outside her nest with the intruder after the aggressive encounter between the males ended.

A distinct winner and loser could be distinguished after each male-male interaction. The loser decamped and did not interact further (45 males), or he was killed and eaten by the winner (3 males). After decamping losing males entered one of the terraria. Sometimes the winner entered a terrarium also, but this was always at least 1 min after the loser. If the female was still in the cage after the loser decamped, the winner always courted. Sometimes 2 or even 3 spiders would enter the same terrarium before the observation period ended, but no interactions took place once inside.

The males that won interactions were larger than the losers (body length of winner minus that of loser: 1.4 ± 0.63 mm; range: 1-3 mm, in 39 cases, smaller only once (difference in body lengths, 1 mm) and the same size in 8 cases ($G = 42.657$, $P < 0.005$).

Four male-male interactions were observed in the context of cohabitation with subadult females. In each case the resident male had been cohabiting with a subadult for 2 to 8 days before the intruding male was introduced into the cage. The resident male departed the nest and threat displays were exchanged in each case. Eventually, one male decamped (resident, 3 cases; intruder, 1); and the other male remained with the nest and cohabited with the subadult female.

OBSERVATIONS IN NATURE

1. A male was standing on a rock, the ground was covered by grass, and the tops of the rocks were above the level of the grass. When another male walked onto a different rock ca. 50 cm away, the first male watched the second walking and turning on the rock and occasionally facing the first male, but only briefly. After ca. 30 sec, the second male stood facing the first for several seconds, whereupon the first male displayed. Immediately the second male also displayed. A few seconds later, the first male ceased displaying, departed his rock, and walked more or less directly toward the rock on which the second male waited. Meanwhile, the second male ceased displaying and resumed walking and turning. After ca. 15 sec, the first male walked onto the rock with the second male, the two males displayed; and after ca. 30 sec, the second male departed from the rock. Several minutes later, I lost sight of him over 2 m away. The winning male walked onto the side of the rock and groomed. A few minutes later, he walked onto the ground and I lost sight of him between the two rocks. There were no nests under the rocks, and no females were seen in the vicinity.

2. A pair of males was exchanging threat displays while standing ca. 3 cm apart on a piece of wood when I discovered them. After briefly embracing and pushing, one male departed; and I lost sight of him more than 1 m away. I inadvertently disturbed the other male, and he ran under the wood. When I overturned the wood ca. 30 min later, I found not only the male, but ca. 30 cm away I found a female inside a nest. This observation suggested that the type of interference envisaged in the laboratory occurs in nature.

DISCUSSION

Aggression.—Evidently interference by an intruding male is likely to lead to more serious consequences for the resident male if it occurs during courtship with a female outside her nest. As with pursuit time, copulation duration, and receptivity (Jackson 1978a, 1980b), this difference is probably related to the female's reluctance to depart her nest. With the female inside her nest, the male is subject to the risk of a prevented copulation due to an intruding male driving him away; but if he wins the aggressive interaction, his chances of subsequently initiating copulation are probably good. In contrast, when the female is outside her nest, interference by an intruding male is likely to prevent copulation, regardless of whether he can drive the intruder away.

Only virgin females were used in this study, and different estimates for these probabilities might be expected if other types of females had been used. For example, maternal females might have been more reluctant to depart their nests. More data are needed, especially for male-male interactions in the context of cohabitation. However, as long as the probabilities estimated here were even roughly accurate, it would seem that the consequences of male interference tend to be more serious to the resident male when the female is outside rather than inside her nest. Unless the frequency of intermale interference is substantially greater with females inside nests, pursuit of females outside nests probably entails greater costs related to this factor; females inside nests, lesser costs.

Crane (1949) reported that males of salticids interacted aggressively more readily and intensively when females were present than when they were absent. This seems likely in the case of *P. johnsoni* also. In three of the 24 male-male interactions with females present outside nests, one of the males was killed by the other. In another case a male was injured but not killed. However, only one male was killed and none simply injured in the 60 male-male interactions outside nests in the absence of females (Jackson 1977).

The presence of females is not necessary for male-male aggression, raising questions about functions of this behavior (Crane 1949). There is no evidence that males maintain territories in a traditional sense, but each male seems to defend a mobile personal space around himself that he strives to keep free of other males. A male with a larger personal space might be less likely to suffer from interference by other males when the opportunity to court and mate arises. However, one might envisage spacing out by simple avoidance behavior. Why do males threaten and fight? Perhaps there are optimal areas for sexual searching which males are hesitant to depart. Also if males have systematic searching routines of some type, these are likely to be disrupted by departure from the area. Whatever the precise cause, if there is an advantage in being the male that remains rather than departs, there would be selection favoring males that interact aggressively and win encounters.

Pursuit Time per Net Benefit.—Estimating P_O , P_N , and P_S is a highly difficult operation. The numerators (time) can be estimated relatively easily; but the denominators (net benefit) need to be expressed in units of fitness, a much more difficult quantity to

measure. The most serious difficulty is that conditions operating in nature need to be evaluated, and this information is not readily available. Quantitative estimates of net benefit will not be attempted here. Instead, an attempt will be made to rank types of females according to decreasing pursuit time per net benefit.

Factors related to benefit (Jackson 1980b) will be considered first. Some females failed to oviposit fertile eggs after copulation, but the probability of this happening was greater after shorter copulations. Following the very lengthy copulations associated with cohabitation, all females in the laboratory oviposited fertile eggs. However, given that the female oviposited fertile eggs at all, there was no relationship between the number she oviposited and the duration of the preceding copulation. Sperm competition can diminish the number of progeny that a male leaves by a given female since inseminated females sometimes copulated with additional males; and when this happened, partial or complete sperm displacement sometimes occurred. After longer copulations, females were less prone to copulate with additional males. Benefit for the male seems to increase with copulation duration, and copulation duration varies with the type of female in a manner such that subadult female inside nest (cohabitation), adult inside nest, and adult outside nest is the order of decreasing benefit.

Expression of the various types of risks to which males are subject (predation, cannibalism, etc.) might be accomplished by using estimates of the probabilities of each type of risk as a weighting factor. Considering cannibalism, for example, a first approximation might be to multiply the male's expected progeny from the female in question by $1 - C$, where C is the probability that she will kill him before copulation. The sum of the male's expected progeny from females that he is likely to encounter in the future should be multiplied by $1 - C$ also. These two quantities should be added next to the male's expected progeny from all females with which he has previously mated.

Various ways in which nests might protect spiders from predators have been discussed elsewhere (Jackson 1976a); and the risks to the male seem greater when courting females outside their nests. Observations of Mathew (1940) and Edmunds (1978) suggest that this factor is especially important in salticids that associate with ants.

Cannibalism is a special type of predation that probably occurs only infrequently in *P. johnsoni*, but the differences in frequencies are such that males pursuing adult females outside nests are probably in the greatest danger (Jackson 1980a). Risks related to interference by other males are probably greater for males pursuing females outside rather than inside nests.

Although various events such as avalanches and large mammals walking past might disrupt interactions between spiders, this type of interference seemed to be too infrequent to be very significant. The longest pursuit time recorded for this species was a 14-day cohabitation (Jackson 1978a). When rocks and pieces of wood were painted and checked monthly in the field for 4 months in succession, it was estimated that the chances of a nest site being overturned during a 14-day period was ca. 1 or 2 in 1000 (Jackson 1976b).

The apparent order of increasing benefit, decreasing risks (cost), and consequently increasing net benefit for the males is as follows: adult females outside nests, adult females inside nests, and subadult females inside nests. Since the numerators, pursuit time, follow the same trend, the ranking of P_o , P_n , and P_s is difficult.

Pursuit times associated with subadult females inside nests (ca. 1 week) are greater than pursuit times associated with adult females outside nests (ca. 2 min) by a factor of ca. 5000 (see Jackson 1978a). Perhaps the numerator of P_i should be viewed as handling

time (the sum of courtship, cohabitation, and copulation durations) instead of simply pursuit time. Adding 14 min for copulation outside nests and 14 hr for copulation after cohabitation, the numerators still differ by a factor of ca. 500.

These estimates are somewhat misleading because all hours of the day and night are not equivalent for males with respect to searching. For example, *P. johnsoni* males remain inside nests at night even if not cohabiting (Jackson 1979). Since the alternative of searching during this period is not available, perhaps the time involved should be subtracted from the measurement of pursuit time. As another example, if the male cohabits during inclement weather, searching would have been prevented or hindered anyway. Apparently, a realistic model should weigh pursuit time according to how much is subtracted from potential search time. However, even after weighting of this type has been taken into account, pursuit times probably still differ by two or three orders of magnitude.

In order for P_s (pursuit time per unit net benefit for males pursuing subadult females) to be less than P_o (adult, outside nest), differences in net benefit would have to be greater than the difference in weighted pursuit time. Considering sperm competition and infertile matings, a difference of an order of magnitude or more seems probable for the number of progeny the male will leave in the two situations; and even greater differences in the magnitude of predation risks might occur. Adult females inside nests seem intermediate with respect to each factor.

A tentative conclusion will be proposed. The trend in net benefit counters the trend in pursuit (or handling) time, and pursuit times per net benefit increase in the following order: P_s (cohabitation with subadult female), P_n (courtship of adult female inside her nest), P_o (courtship of adult female outside her nest).

In the mating strategy of *P. johnsoni*, there are three types of females pursued by males, one of which should have the smallest or optimal P_i . If the optimal type of female is "subadult inside nest," why do males also pursue the two suboptimal types? Also, males do not pursue every type of female that they encounter. For example, males of the sparassid spider *Isopeda immanis* are reported (Clyne 1971, Coleman 1938) to remain with subadult females outside their nests and mate when they mature. In other words, males of *I. immanis* apparently pursue subadult females outside nests, a type of female not pursued by males of *P. johnsoni*. The most that occurs when an adult male of *P. johnsoni* encounters a subadult female outside her nest is a brief display followed by a speedy departure (Jackson 1977).

The general question that arises is analogous to one concerning the optimal diet of a predator. There are various types of females that males of a species will encounter. What set of these do they pursue? As in optimal foraging theory (MacArthur 1972, Pyke *et al.* 1977), we begin by ranking types of females, higher rank corresponding to smaller P_i . Beginning with the type of female with highest rank, additional ones are added to the set ("pursued females") in decreasing rank order (increasing order of P_i). This is continued so long as benefit divided by handling times with each addition is greater than would be the case without the addition. The optimal set of pursued females is one for which the next addition reverses the inequality. For *P. johnsoni* adding subadult females outside nests may reverse the inequality because net benefit is very small due to high risks of predation, interference by other males, and physical disturbances that cause males to lose visual contact with subadults amongst the vegetation and rocks in the habitats of the spiders.

A surprising property of optimal foraging theory is that whether or not a type of prey (type of female) is pursued is independent of the abundance of that type of prey

(female). The important factor is the absolute abundance of the types of higher rank. Following this line of thought, pursuit of subadult females inside nests is predicted even if this type of female is rare in a population. However, if the density of subadult and/or adult females inside nests is very high in a population, pursuit of adult females outside nests might not occur. Populations with differing densities and phenology have been studied (Jackson 1978b), but males from all of these pursued each of the three types of females. However, there were interpopulational differences in courtship persistence by males pursuing adult females outside nests, and optimal foraging theory has been discussed in reference to this (Jackson 1980c).

Concepts of optimality have generated insights concerning predation that would not have arisen so readily from more traditional viewpoints. Pyke *et al.* (1977) expressed optimism concerning the future of this relatively new approach in the study of predation. Similar approaches have been initiated in the study of mating behavior (Parker 1974), and similar optimism seems warranted.

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THE EVOLUTION AND BIOGEOGRAPHY OF THE MYGALOMORPH SPIDER FAMILY HEXATHELIDAE (ARANEAE, CHELICERATA)

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ABSTRACT

The family Hexathelidae is newly erected. Three subfamilies are recognized: Plesiothelinae, for the monotypic Tasmanian genus *Plesiothele*; Macrothelinae, confined to *Macrothele*, *Porrhothele* and *Atrax*; and the Hexathelinae include *Hexathele*, *Scotinoecus*, *Bymainiella*, *Paraembolides*, gen. nov. and *Terania*, gen. nov. The synapomorphic character required for group membership is numerous labial cuspules. Using the size of the anterior lateral spinnerets, the development of megaspines on the first tibia of males, the paraembolic apophysis, and shape of the labium and other characters, the evolution of subfamilies, genera and some species is discussed using Hennigian principles. A biogeographic hypothesis is proposed using the vicariance events of Plate Tectonic theory. The sister group of the Hexathelidae is the Dipluridae, and the sister group of both is the Mecicobothriidae. The subfamily Ischnothelinae is erected to receive those genera of the traditional Macrothelinae that have no labial cuspules.

INTRODUCTION

The Mygalomorphae are an important group of spiders that have been neglected in discussions of evolution and biogeography. They are important as they possess features widely regarded as plesiomorphic in spiders, and they give a major perspective to evolutionary hypotheses. Pocock (1903) is the only arachnologist of wide knowledge to propose a theory to explain the contemporary distribution of mygalomorphs. Unfortunately, Pocock did not depart from the widely held views of faunal origins of his time, whose protagonists maintained that southern migrations of northern species occurred across land bridges, presumed to have been static for some time.

Evolutionary hypotheses are lacking, and even now an acceptable phylogeny of the Mygalomorphae does not exist. Classificatory keys required ease of application, and monothetic groups, which were usually made up of paraphyletic taxa sharing only plesiomorphic characters, resulted. With Hennig (1966) began the widespread acceptance of phylogenetic systematics, in which a shared derived character is needed to join two sister groups. This allowed the formulation of empirically testable hypotheses.

The weakness of the cladistic (= phylogenetic sensu Henning) methodology lies in the decision about the direction of character change, upon which Brundin (1966) remarked, may be completely right or wrong - there being no alternative. This apparent weakness of cladistic methodology becomes its strength, as further characters may then be used to test the polarity of characters originally used, and so test the overall cladogram.

Within the Dipluridae, the Hexathelinae are historically regarded as primitive spiders and are diagnosed by primitive characters. However, their patristic similarity to one another suggests monophyly and the Mesothelae (= Liphistiomorphae, see Platnick and Gertsch 1976) attest the possibility of plesiomorphic taxa being monophyletic. Raven (1978) re-examined the sub-family Hexathelinae taxonomically, and arrived at conservative conclusions about the ranks of certain taxa. At that time the theory proposed herein was in its genesis, and the conclusions about the phylogenetic relationships of the genera involved were tempered.

In this study, I shall present evidence which strongly suggests that, at least in the Hexathelinae, the paraembolic apophysis - the probable homologue of the conductor, is present only in more derived genera, and is thereby apomorphic.

Considerable attention has been recently directed to the phylogenetic position of the Liphistiidae, and in cladistic analyses, Platnick and Gertsch (1976) and Kraus (1978) have used the unique sexual morphology of *Liphistius* and related genera to support their theory. The male liphistiid palpal bulb appears to be a surprisingly complex structure for a generally plesiomorphic group of spiders. Consequently, the traditional interpretation of this enigmatic complexity has generally been that complexity infers apomorphy. Gertsch (in Platnick and Gertsch 1976) and Kraus (1978) present the alternative hypothesis that, in fact, the liphistiid palp is plesiomorphic, and that less complex palpal bulbs have been the result of multiple parallel reductions of structures - not necessarily an equivalent process to simplification. The basis of this hypothesis is the correlation of the bipartite male palpal bulb with the bipartite nature of the corresponding female genitalia, and distribution of the bipartite condition in the atypids and hypochiloids as well as liphistiids.

SYSTEMATICS

Family Hexathelidae (Simon, 1892)

Diagnosis.—Mygalomorph spiders with eight eyes and a transverse fovea; carapace lacking hairs. One or two rows of teeth on the cheliceral furrow; no rastellum. Maxillae longer than wide; ectal anterior corner with slight angular production and with serrula; armed with numerous cuspsules. Labium square to wide; armed with numerous cuspsules. Sternum separated from labium by sigilloid groove; six sigilla. No leg scopula in females. Three claws; one row of teeth on superior claws; inferior claw well developed. Trichobothria in two rows on tibiae, one row on metatarsi, and one irregular to straight row on tarsi. Trichobothrial bases collariform. Four to six spinnerets; apical segment of posterior laterals digitiform.

Male palp simple or with paraembolic apophysis; anterior tibiae of males modified. Internal genitalia of females with one or rarely two lobes on each side - the lobes uni- or multilocular.

Remarks.—The elevation of this family is based upon the synapomorphous possession of numerous labial cuspsules by all of its members. The family is divided into 3 sub-

families: Hexathelinae, Macrothelinae and Plesiothelinae.

The sister group of the Hexathelidae.—The sister group of the Hexathelidae is the Dipluridae, and together these two families form the sister group of the Mecicobothriidae. This is based upon the absence of abdominal tergites in the former families. These three families may be united in the presence of a maxillary serrula in most genera (see Platnick 1977). In the Dipluridae, labial cuspules are rarely present, and when present are very few; and all diplurid genera so far examined have corrugiform trichobothrial bases. All hexathelid genera have collariform bases. Although the corrugiform condition may not be a synapomorphy for the diplurids, it is another difference from the Hexathelidae.

Subfamily Hexathelinae (Simon, 1892)

Diagnosis.—Six spinnerets. True megaspines present on first tibiae of males. Caput of females low.

Checklist of genera.—*Hexathele* Ausserer, 1871; *Scotinoecus* Simon, 1888; *Bymainiella* Raven, 1978; *Terania*, gen. nov.; *Paraembolides*, gen. nov.

Remarks.—The genera constituting this subfamily are unchanged from Raven (1978), except that *Plesiothele* is removed, and *Bymainiella* is now divided into three genera. The reasons for these changes will be made clear below. A 'megaspine' is a thickened spine which crowns an apophysis; it replaces the term 'spur' which is misleading (Raven, 1980).

The diagnoses of *Hexathele* and *Scotinoecus* are those given previously (Raven 1978), except that *Scotinoecus* may have as few as 10 labial cuspules (pers. obs.).

Bymainiella Raven

Bymainiella Raven 1978: p. 56. Type-species by subsequent designation: *Hexathele terraereginae* Raven, 1976.

Diagnosis.—Males with a prominent distal megaspine on tibia I, interfacing with a prolateral metatarsal flange. Male palpal bulb pyriform or with a broad protuberance. Female internal genitalia with one bifurcate lobe on each side. Tarsal trichobothria in a single line. Labium wider than long. Up to thirty cuspules on labium. No spines on leg tarsi.

Checklist of species.—*Hexathele terraereginae* Raven, 1976 (type-species); *Bymainiella lugubris* Raven, 1978; *Bymainiella polesoni* Raven, 1978; *Bymainiella monteithi* Raven, 1978.

Remarks.—This is the *Bymainiella terraereginae* species-group of Raven (1978).

Terania, gen. nov.

Diagnosis.—Males with a single distal megaspine on a raised apophysis on tibia I; metatarsus I proximally excavate, without a flange; palpal bulb pyriform. Labium almost as long as wide or wider. Spines usually present on all tarsi. Tarsal trichobothria in a single line. Up to thirty cuspules on labium.

Type-species.—*Hexathele montana* Hickman 1927

Etymology.—*Terania* is a euphonious combination of letters which conveys the earth; the gender is feminine.

Remarks.—Apart from the type-species, this genus includes only *Bymainiella otwayensis*. *Paraembolides tubrabucca* shares only plesiomorphic characters with the species of *Terania*, and is removed to *Paraembolides*.

Paraembolides, gen nov.

Diagnosis.—Males with a single distal megaspine, but not on a raised apophysis, on tibia I, no metatarsal flange; palpal bulb with paraembolic apophysis. Labium much wider than long. Spines absent from anterior tarsi. Tarsal trichobothria in a single line. Up to thirty cuspules on labium.

Checklist of species.—*Bymainiella boycei* Raven, 1978 (type-species); *Bymainiella boydi* Raven, 1978; *Bymainiella brindabella* Raven, 1978; *Bymainiella cannoni* Raven, 1978; *Bymainiella grayi* Raven, 1978; *Bymainiella montisbossi* Raven, 1978; *Bymainiella tubrabucca* Raven, 1978; *Bymainiella variabilis* Raven, 1978.

Etymology.—This name is derived from the paraembolic apophysis which characterizes the group; the gender is feminine.

Remarks.—Although *Paraembolides tubrabucca* was originally regarded as a sister species of *Terania montana*, the presence of a small paraembolic process on the former indicates affinities with species placed in *Paraembolides*.

Subfamily Macrothelinae (Simon, 1892)

Diagnosis.—Four spinnerets. Labium almost as wide as long or longer. Cuspules on labium typically very numerous. True megaspines absent on tibia I, tibia I densely spined and incrassate; may have mid-ventral apophysis on tibia II.

Checklist of genera.—*Macrothele* Ausserer, 1871; *Porrhothele* Simon, 1892; *Atrax* Pickard-Cambridge, 1877.

Remarks.—Prior to this study the Macrothelinae included *Allothele*, *Cethegus*, *Evagrella*, *Evagrus*, *Holothele*, *Ischnothele*, *Lathrothele*, *Linothele*, *Phyxioschaema* and *Thelechoris*, as well as those listed above. The type-species of *Holothele* and *Linothele* have been examined. *Holothele* is a theraphosid, and probably is a synonym of *Stichoplastus*, and *Linothele* is a junior synonym of *Diplura*.

The sub-family Macrothelinae is limited to those genera with cuspules on the labium as well as on the maxillae. However, such genera also have digitiform posterior lateral spinnerets, a raised caput, and usually have few hairs on the carapace. This is in contrast to the *Evagrus*-like genera which have long posterior lateral spinnerets, a low caput, and a hirsute carapace. The redefinition of the Macrothelinae leaves those diplurids with four spinnerets and one row of teeth on the superior claws without a subfamily group name. I propose *Ischnothele* as the nominate genus, as Pickard-Cambridge (1897) had previously suggested.

Macrothele Ausserer

Macrothele Ausserer 1871: 181. Type-species by original designation: *Mygale calpeiana* Walckenaer 1805.

Diagnosis.—Posterior sternal sigilla much larger than anterior pairs. A row of teeth on cheliceral promargin only or with an additional row of smaller teeth on retromargin. Tibia I of males incrassate. Spines present on tarsi.

Remarks.—Some *Macrothele* species have a reduced number of labial cuspules whereas most species of this and other macrothelinid genera have numerous cuspules. The species constituting this genus have not been critically examined and are as listed by Bonnet (1959) except that *M. aculeata* is excluded because it is a ctenizid (Main, pers. comm.).

Porrhothele Simon

Porrhothele Simon 1892: 182. Type-species by original designation and monotypy: *Mygale antipodiana* Walck. 1837.

Diagnosis.—Posterior sternal sigilla small, marginal. A row of teeth only on cheliceral promargin. First tibia of males incrassate. No spines on leg tarsi.

Remarks.—Forster and Wilton (1968) give an excellent revision of this genus, consequently no extensive diagnosis is necessary. *Porrhothele* is very similar to *Macrothele* in sexual morphology; however, they may be readily distinguished in that *Porrhothele* has no spines on the leg tarsi.

Atrax Pickard-Cambridge

Hadronyche Koch 1873: 463. Type-species by original designation and monotypy: *H. cerbera* Koch 1873.

Atrax Pickard-Cambridge, O. 1877: 26. Type-species by original designation and monotypy: *A. robustus* Pickard-Cambridge 1877.

Styphlopis Rainbow 1913: 6. Type-species by original designation and monotypy: *S. insularis* Rainbow 1913.

Euctimena Rainbow 1914: 249. Type-species by original designation and monotypy: *E. tibialis* Rainbow 1914.

Pseudoatrax Rainbow 1914: 261. Type-species by original designation and monotypy: *P. moreaui* Rainbow 1914.

Poikilomorpha Rainbow 1914: 265. Type-species by original designation and monotypy: *P. montana* Rainbow 1914.

Anepsiada Rainbow and Pulleine 1918: 167. Type-species by original designation and monotypy: *A. ventricosa* Rainbow and Pulleine 1918.

Diagnosis.—Posterior sternal sigilla large. A row of teeth on both cheliceral margins. First tibia of males not incrassate.

Remarks.—*Hadronyche* is the senior subjective synonym of the medically infamous *Atrax*. However, a submission is believed to be before the International Commission for Zoological Nomenclature for the suppression of *Hadronyche*; the genus is also currently being revised (M. Gray, in litt.).

Atrax is probably the most contentious genus of this family. However, on the basis of its derived characters it is not closely related to any other group in the Dipluridae. Moreover, its affinities with other genera of similar facies, such as the atypoid genera, must be discounted as the maxillae are not sufficiently modified to allow it to be a member of that group. Other characters that are discussed below, such as the presence of a maxillary serrula, indicate that *Atrax* is more closely related to the Hexathelidae and Dipluridae.

Subfamily Plesiothelinae, new sub-family

Diagnosis:—Six spinnerets. Terminal segment of anterior lateral spinnerets enlarged, and apical segment domed. First tibia of male without modifications; metatarsus I bent; palpal bulb pyriform, with a short twisted embolus.

Remarks:—This subfamily has, as its only member, the monotypic genus, *Plesiothele* Raven 1978.

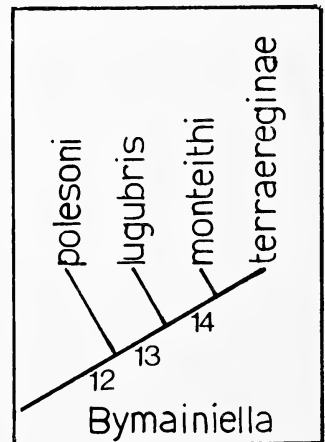
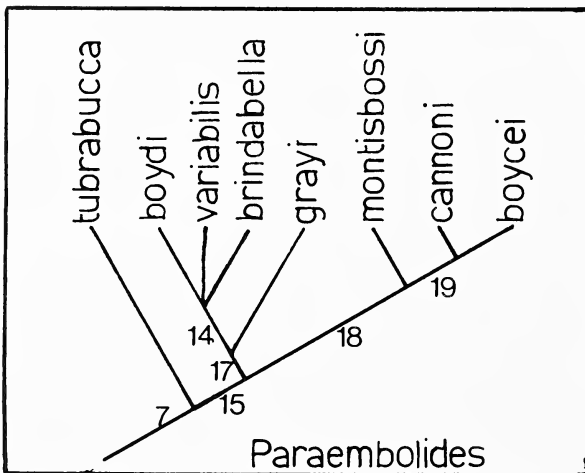
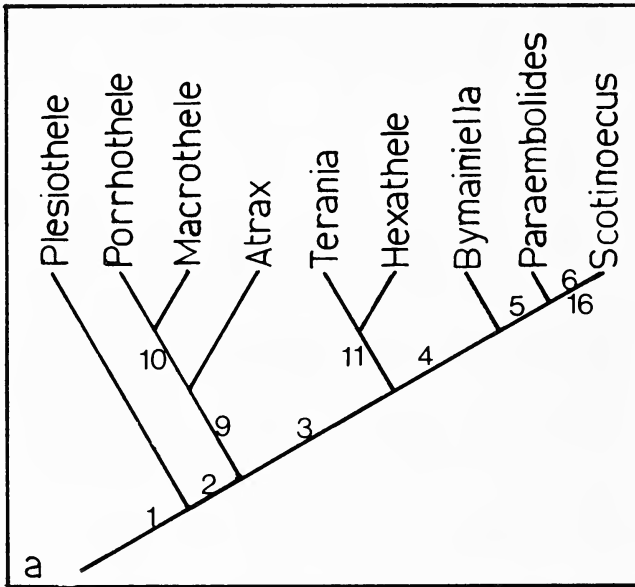


Fig. 1.—Cladograms of the family Hexathelidae. Table 1 shows characters associated with numbers.

THE CONSTRUCTION OF THE CLADOGRAM

The members of each subfamily and genus are taken from the cladogram (Fig. 1a) of the family. The construction of the cladogram, in following the principles of phylogenetic systematics expounded by Hennig (1966) and Brundin (1966), requires that each group must have derived characters (Table 1) uniquely shared by the members of that group. In the cladogram, immediately below the fusion point of two sister groups, is the number of the character that is regarded as the synapomorphy of the taxa above that point. The term 'ancestor', as used here, refers to a hypothetical taxon not an individual.

Characters

1. The maxillary and labial cuspules.—In the Mygalomorphae the presence of numerous cuspules on the maxillae is unique, and thus it may be this character, which although polythetic, is the autapomorphy of the Mygalomorphae. As confirmation of this, cuspules do not occur in the Mesothelae, thus their presence in the Mygalomorphae may, by outgroup comparison, be regarded as apomorphic. This does not invalidate the reverse polarity indicated by Platnick and Shadab (1976) for the Actinopodidae, because that is in a widely separated clade, in which the loss of cuspules may be secondary.

The dense (= closely grouped) spination of the labium is, on the other hand, an unusual character. Numerous labial cuspules are present in migids, barychelids and theraphosids, but these clades are widely separated from the group under study. Within the three-clawed Mygalomorphae, only the Hexathelidae and the ctenizid genera, *Bessia* and *Spiroctenus*, have numerous labial cuspules. Thus, within the Dipluridae (s. lat.) and Mecicobothriidae, regarded as sister groups by Platnick (1977) in the joint possession of a maxillary serrula, the Hexathelidae is the only group that has numerous cuspules on the labium. It is upon this basis that the Hexathelidae is regarded as a monophyletic group.

2. The male palpal embolus.—In the Mygalomorphae, the embolus is commonly elongate to whip-like; in the Mesothelae, the embolus is short; whereas in the Araneomorphae, the apomorphic sister group of the Mygalomorphae, the embolus is most widely elongate or whip-like. Thus, by out-group comparison and abundance, the short embolus is regarded as a plesiomorphic retention, and the elongate embolus derived. An important aspect of this character is that, although it is clearly apomorphic, its widespread presence in the Mygalomorphae strongly indicates that it may have independently evolved to the same condition many times.

3. The modification of the first leg of the male.—The megaspines which occur on one or both pairs of anterior legs in male mygalomorphs, also occur in some araneomorphs, but are unusual in their function of maintaining the fangs of the female open during mating. Such megaspines do not occur in the more plesiomorphic Mesothelae, and are therefore considered apomorphic. Furthermore, the leg spination of immature males is identical to that of conspecific females, and it is only in the final moult of the male that spine dimorphisms and megaspines, if present, appear. Thus, the spination of females is believed to be more plesiomorphic than that of males.

The usual spination of the first tibia of female hexathelids is two ventral subdistal pairs followed apically by four spines set along the ventral tibial edge. A similar condition occurs in *Plesiothele*, and is regarded as plesiomorphic. As remaining taxa of the Hexathelidae have at least a group of numerous spines on the first tibia of males, this state is

Table 1.—Characters used in cladograms.

Plesiomorphic state	Apomorphic state
1. No labial cuspules	Numerous labial cuspules
2. Short embolus	Long embolus
3. Male tibia I without megaspines	Male tibia I with megaspines
4. Labium about as long as wide	Labium wider than long
5. Paraembolic apophysis absent	Paraembolic apophysis present
6. Anterior lateral spinnerets equal length to posterior medians	Anterior laterals clearly shorter than posterior medians
7. Spines present on anterior tarsi	Spines absent on anterior tarsi
8. Metatarsus I of males straight	Metatarsus I of males angular
9. Six spinnerets	Four spinnerets
10. Tibia I of males cylindrical	Tibia I of males incrassate
11. Metatarsus I of males cylindrical	Metatarsus I of males excavate
12. No flange on male metatarsus I	Flange present on male metatarsus I
13. ♀ patella III less than tibia III	♀ patella III greater than or equal to tibia III
14. 6-12 spines on ♀ metatarsus III & IV	4 spines on ♀ metatarsus III & IV
15. Paraembolic apophysis short	Paraembolic apophysis well-developed
16. Paraembolic apophysis thorn-like	Paraembolic apophysis spiniform
17. No hairs behind foveal bristles	Hairs present behind foveal bristles
18. No bristles lateral of eyes	Numerous bristles lateral of eyes
19. Paraembolic apophysis coniform	Paraembolic apophysis acute

considered an apomorphy that is correlated with the suggested apomorphy of the elongate embolus.

The character specifically involved here is 'true' (i.e. immovable) megaspines, and is probably the polythetic synapomorphy of the Hexathelinae, since all members have true megaspines and not simply a tibial apophysis thickly clad with spines, as in *Atrax formidabilis*.

4. The relative dimensions of the labium.—In the relatively plesiomorphic taxa to *Hexathele* on the cladogram, the width of the labium approaches its length, whereas in the more derived taxa the labium is considerably wider than long. Thus, in being confined to apomorphic taxa, a wide labium is regarded as apomorphic. The liphistiid labium is wide, and the araneomorph labium is highly variable.

5. The paraembolic apophysis.—This character requires some introduction as this term, that applies to an angular process arising adjacent to the embolic origin, was recently introduced by Raven (1978). In the male of *Scotinoecus fasciatus*, it was regarded as a 'conductor' by Schiapelli and Gerschmann de Pikelin (1968). It also occurs as a clearly supportive apophysis in some *Masteria* where, as a unilaterally grooved process, it distally supports the embolus (see Raven 1979); in some barychelid genera, it is present in a nominal state. In view of its widely dispersed presence in the Mygalomorphae, the paraembolic apophysis may be a plesiomorphic retention, or the result of parallel derivation in diverse clades; however, in the Hexathelinae it is apomorphic.

In the Atypidae, Antrodiaetidae and Mecicobothriidae, the embolus is usually entirely enclosed in a chitinous sheath, regarded as a conductor. It is here proposed that the paraembolic apophysis is the analogue of the conductor.

The Gertschian Theory: Gertsch (in Platnick and Gertsch 1976) has proposed that the bipartite palp of the Atypoidea and the palp of the Liphistiidae are plesiomorphic. This conclusion is based upon the correlation of the male palp with female characters. Thus, in contrast to the hypothesis proposed here, the parembolic apophysis would be interpreted as a more apomorphic reduction from the atypoid conductor. Also, the unencumbered palpal bulb so widespread in the Mygalomorphae, would be regarded as the most apomorphic state.

Gertsch states that: 'Two receptacles on each side is the standard number for the liphistiids, the three other atypoid families, the most generalized of the diplurids (*Scotinoecus* and *Hexathele*), and the primitive araneomorph spiders, the *Hypochilidae* and related families. . . . thus, in *Hexathele*, the paired receptacles persist on each side even though a single embolus is now present.'

Kraus (1978) uses the '2 + 2' terminology for the type of internal genitalia widespread in the Mygalomorphae and for the type in *Hypochilus* in which the two receptacula on each side join before discharging into a common atrium (through fusion?). Although Gertsch (in Platnick and Gertsch 1976) also used this '2 + 2' terminology, he restricts it to the typical configuration seen in *Atypus* and the Antrodiaetidae in which each of the four or more receptacula (2-11 on each side, Kraus 1978) discharge separately into the atrium.

Schiapelli and Gerschman de Pikelin (1962) have shown that the female *Liphistius* has complex internal genitalia, and hardly homologous with those of the Antrodiaetidae (see Coyle 1968, 1971, 1975). Moreover, of the two species of *Scotinoecus*, one has two separate receptacles on each side, and the second species has only one bifurcate receptacle on each side. In other hexathelids and the Dipluridae, no genus is known to have two receptacles on each side - all have one. Some *Masteria* have two lobes on each side although these are joined as part of a united receptacle leading to a single atrium (Raven 1979). Thus, although these two characters, the bipartite palp and the two pairs of

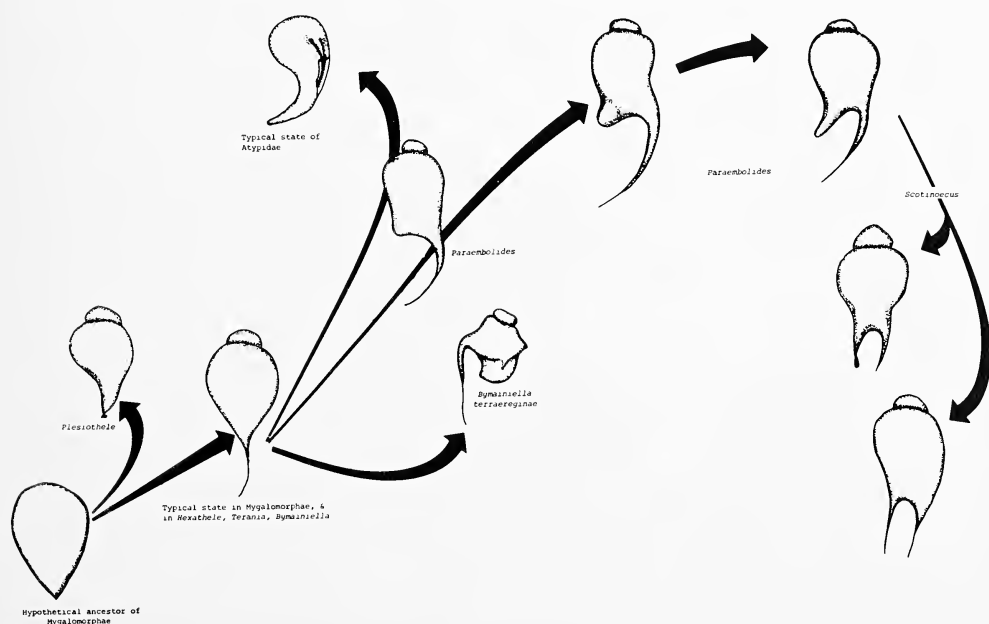


Fig. 2.—Evolution of the male palpal bulb in the Hexathelidae.

receptacles in the female, are correlated, neither can unequivocally indicate a direction of change and a third character must be introduced. This is the anterior lateral spinnerets.

6. The reduction of the anterior lateral spinnerets.—Within the Macrothelinae and Hexathelinae, the anterior lateral spinnerets exhibit a clearly reducing trend. In the Australian and New Zealand genera, the anterior lateral spinnerets are two-segmented, but are as large as, or larger than, the posterior median spinnerets; whereas in *Scotinoecus*, the anterior lateral spinnerets are strongly atrophied, especially in *S. cinereopilosus*. Ontogenetically, and by out-group comparison, the evolutionary trend of the anterior lateral spinnerets is toward absence. Finally, the result is the widespread four-spinnereted state. Thus, the atrophied anterior laterals are the most apomorphic state of the spinnerets seen in the Hexathelinae. In the Macrothelinae, the anterior lateral spinnerets are completely lost.

Correlated with the reduction in size of the anterior lateral spinnerets in the Hexathelinae, is the corresponding increase in the length of the paraembolic apophysis. In *Paraembolides*, the paraembolic apophysis varies from a low apophysis to a very acute process; in *Scotinoecus*, the paraembolic apophysis is maximally elongate. This strongly suggests that the development of the paraembolic apophysis is apomorphic within the Hexathelinae.

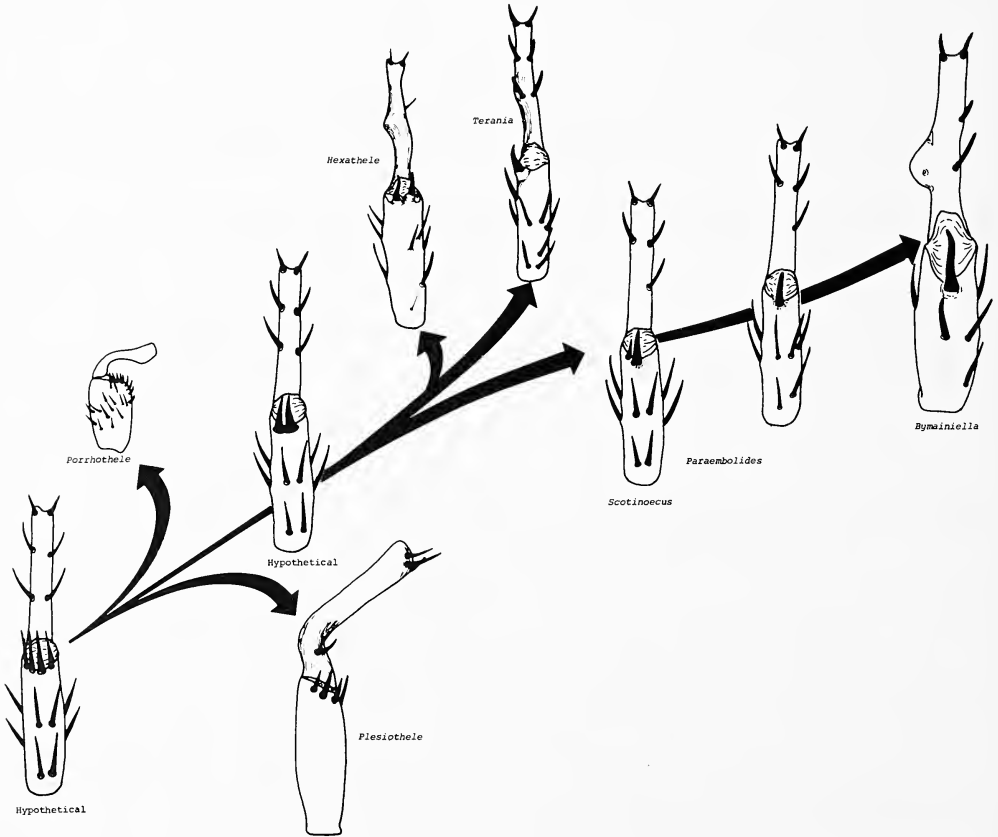


Fig. 3.—Evolution of the first tibia and metatarsus of males in the family Hexathelidae.

7. Anterior tarsal spines.—Anterior tarsal spines are functional in spiders which burrow, and are present in many mygalomorphs and in the Mesothelae. As both *Paraembolides* and *Scotinoecus* no longer excavate burrows, but occupy existing excavations, the presence of anterior tarsal spines is believed to be a plesiomorphic retention in *Scotinoecus*, and their absence in *Paraembolides* is the synapomorphy. The loss of tarsal spines is regarded as a parallelism, having occurred independently in *Bymainiella* and *Paraembolides*.

At this stage, the synapomorphies of all main stem groups have been discussed; the discussion of the synapomorphic characters of lateral clades follow.

8. The first metatarsus of the male.—In *Plesiothele*, the first metatarsus of the male is bent or sinuous, and uniform in diameter throughout its length. Because this condition is unique to *Plesiothele*, and as further shown by out-group comparison with male Mesothelae in which the metatarsi are straight and unmodified, it is regarded as apomorphic.

9. Four spinnerets.—All other hexathelinids have six spinnerets, thus the four spinnereted state of the Macrothelinae is apomorphic. The argument involved here is a logical extension of that given in 6.

10. The first tibia of the male.—In *Porrhothele* and *Macrothele*, the first tibiae of males are incrassate and densely covered with spines. This is unique within the family, and is thereby regarded as apomorphic. The autapomorphies of *Atrax*, *Macrothele* and *Porrhothele* are: strong teeth on both margins of the cheliceral furrow; moderately sized teeth on the retromargin of the cheliceral furrow; and the absence of tarsal spines respectively.

11. The proximal excavation of metatarsus I of the male.—The synapomorphy of *Hexathele* and *Terania* is the proximal excavation of the first metatarsus of males, which is maximally expressed in *Hexathele*. This should not be confused with the proximal metatarsal flange which occurs in *Bymainiella*, in which no reduction of the proximal diameter of the metatarsus is present.

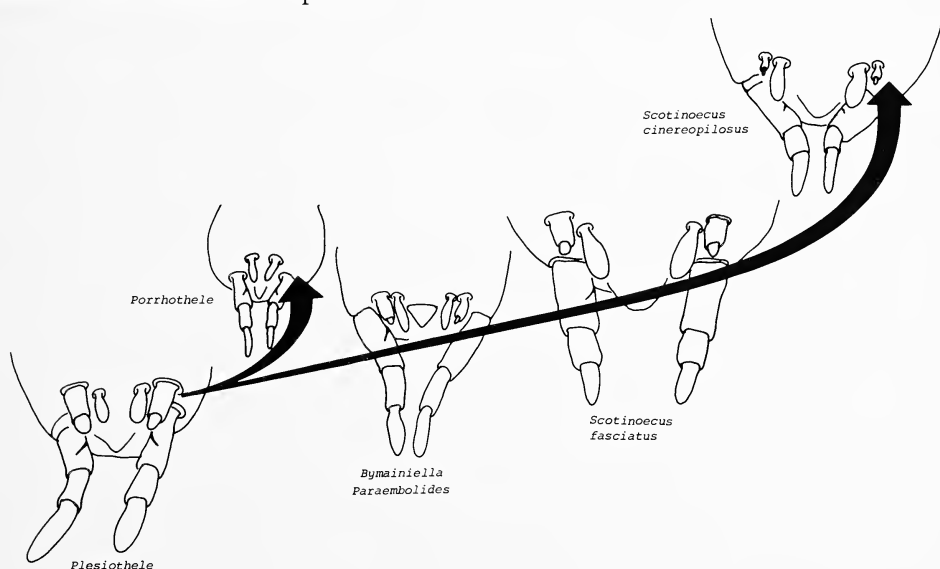


Fig. 4.—Evolution of the anterior lateral spinnerets in the family Hexathelidae.

12. The proximal metatarsal protuberance in the male.—Only in *Bymainiella* do males possess a conspicuous flange on the first metatarsus, and associated with this is the large sinuous tibial spur; because of their uniqueness these characters are regarded as apomorphic.

13. The equality of patella and tibia of females.—Throughout the Hexathelidae, females have a longer tibia than patella of the anterior legs, but in *Bymainiella lugubris*, *B. monteithi* and *B. terraereginae* the patella and the tibia are at least subequal; this is taken to be the apomorphic character which defines this species group. It should be noted here, that in burrowing mygalomorphs it is not unusual to find that the third patella is longer than the tibia. However, in these three *Bymainiella* species which exhibit this condition the two anterior pairs of legs also share this state.

14. Spination of the posterior metatarsi of females.—Four spines, dorsally and laterally on the posterior metatarsi, are more ordered than the more numerous and disordered state seen widely in the group, and it is this ordered condition which is regarded as the apomorphic state. The plesiomorphic state is from 6-12 spines on the metatarsi, and with different counts on each side of the spider.

15. The autapomorphies of *Scotinoecus*.—Two characters indicate the derived nature of this genus: the elongate nature of the paraembolic apophysis, and reduction of the anterior lateral spinnerets.

16. The paraembolic apophysis.—The paraembolic apophysis, as a vestigial mound or as an acute apophysis, occurs in both *Paraembolides* and *Scotinoecus*; it is most prominently developed in the latter, and in *Paraembolides tubrabucca*, occurs in the most plesiomorphic state - as a low triangular bump. Any states more highly developed than that of *P. tubrabucca* are regarded as more apomorphic, by an extension of argument 5.

A Synthesis

The Hexathelidae appear to be a monophyletic group which are characterised by the synapomorphous presence of numerous labial cuspules. Because some genera have retained anterior lateral spinnerets, they have been long regarded as the most plesiomorphic diplurids.

The short embolus and large anterior lateral spinnerets retained by *Plesiothele* place it basally in the phylogeny, prior to the development of true megaspines on male tibiae. With the loss of the anterior lateral spinnerets arose the ancestor of the Macrothelinae, now confined to *Atrax*, *Macrothele*, and *Porrhothele*. In the sister group of the Macrothelinae, the male ancestor of the Hexathelinae had already lost the two most lateral ventral spines on the tibiae, and the median pair of spines were undergoing an associated thickening. This male ancestor had two megaspines on the first tibiae and an unmodified metatarsus. From this male arose two groups. The apomorphic sister group consisted of *Bymainiella*, *Paraembolides* and *Scotinoecus*, in whose ancestor the labium was already wider than long and continued to widen. The plesiomorphic sister group consisted of *Hexathele* and *Terania*. The male ancestor of this group developed a proximally excavated first metatarsus, and retained a square labium.

The male ancestor of *Paraembolides* and *Scotinoecus* developed a paraembolic apophysis on the palpal bulb, and in the plesiomorphic ancestral sister genus, *Bymainiella*, males developed a proximal metatarsal flange on the first leg. In the 'Hexathele' clade, *Terania* lost one of the megaspines; the associated apomorphies in *Hexathele* were the distally alternating rows of trichobothria and the deeply excavate metatarsus of the male.

HISTORICAL BIOGEOGRAPHY OF THE HEXATHELIDAE

Spiders have often been regarded as poor subjects for biogeographic studies, and this is directly attributable to their well known high vagility. The rule for smaller and more readily dispersing spiders is indiscriminately considered the rule for all. However, the more cryptozoic or positively geotropic forms must be regarded as migrators. Thus, prominent past araneologists have maintained that many groups, such as the Mygalomorphae, owe their present distribution solely to their terrestrial dispersal (Pocock 1903), and presumably to transoceanic journeys on log rafts.

Platnick (1976) has indicated some of the practical objections to aerial dispersal and transoceanic colonization. Briefly, the problems are the prolonged dessicating atmosphere, coupled with the non-availability of water, and the astronomically remote chances of a juvenile successfully colonizing a suitable habitat, with low competition for resources, until mating had occurred with another such matured specimen. Although very small, the possibility of mygalomorphs colonising by log rafting cannot be dismissed. Indeed a gravid female of an arboreal mygalomorph species could survive a raft voyage, if the entire log or tree, in which the spiders burrow was already made, was dislodged, and became water-borne. But the dispersal hypothesis is not testable and is therefore not scientific (Platnick 1976, Platnick and Nelson 1978).

Further evidence suggesting that the mygalomorphs do not raft is their absence from the Sandwich Islands, Hawaii (Simon 1904) and indeed, most other oceanic islands. There are at least five notable exceptions to this. The diplurid genus, *Cethegus*, occurs in Australia and New Caledonia, although it does not occur in New Zealand (Main, in press). *Masteria*, another diplurid, and *Idioctis*, a barychelid, are known from the Samoan Islands; *Masteria* is also known from northern Australia, New Guinea, the Phillipines, Venezuela, the Caribbean islands and Chile (Raven 1979). *Migas* is known from Australia, New Zealand and New Caledonia. Zapfe (1961) describes *Migas* from South America but, from the description, it cannot be *Migas*. *Encyocrypta* occurs on New Caledonia and in Australia. In these cases, New Caledonia and the Samoan Islands are not true oceanic islands as they were once part of an Australian plate, which separated in the Cretaceous, and was uplifted in the mid-Eocene (Raven and Axelrod 1972). Furthermore, the barychelid found on Samoa occurred on the fringe of the sea, and was probably one of the few exceptions that proves the rule (Marples 1951).

The distribution of the Hexathelidae.—Of the three subfamilies, the monotypic subfamily Plesiothelinae is endemic to Tasmania. The Macrothelinae consist of *Macrothele*, which occurs throughout Laurasia and in Central Africa, and the Oriental region; *Porrothele* which is endemic to New Zealand and is the sister group of *Macrothele*; and *Atrax*, which occurs throughout east coastal Australia from Tasmania northwards (Hickman 1964) to 24° North. The affinities of all species described by Rainbow (1920) suggest that the Papua locality was an error and thus the records of *Atrax* from Papua, and probably also those from the Solomon Islands (Rainbow 1913) and Cloncurry (Rainbow and Pulleine 1918) should be disregarded. The Hexathelinae include *Hexathele*, which is endemic to New Zealand; its sister group, *Terania* is known only from southern Australia including Tasmania; *Bymainiella*, which occurs in south central coastal Australia; *Paraembolides*, which is known from New South Wales and southern Queensland, Australia; and *Scotinoecus*, endemic to South America.

A biogeographical hypothesis.—Platnick and Nelson (1978) have provided several axioms for the testing of biogeographical hypotheses. However, the complexity of

possible events in historical biogeography fills the reconstruction of these events with secondary, non-testable hypotheses involving dispersal of organisms into areas already occupied by other members of the monophyletic taxon.

The ancestor of the Hexathelidae arose in East Antarctica in the early Jurassic, when Gondwanaland was still entire. This spider had dense labial and maxillary cuspules and six spinnerets, and the male had no tibial megaspines. Before Africa rifted northward in the mid-Jurassic to mid-Cretaceous (Veevers et al. 1971), this group radiated into Africa, India and throughout Antarctica.

Plesiothele arose soon after, near Tasmania, and probably had several related species. From the present localized distribution of this genus, it appears that it had low powers of vagility and its distribution was severely effected by the extent of Pleistocene glaciation in Tasmania.

In the ancestral sister group of *Plesiothele*, the anterior lateral spinnerets were beginning to reduce, but in other features it differed little from the ancestor of the Hexathelidae. From this ancestor arose two groups. One was a *Macrothele*-like ancestral spider group which had four spinnerets but no male tibial megaspine, which arose in East Antarctica and dispersed westward toward New Zealand and Australia. This is indicated by the contemporary widespread presence of *Macrothele* in Laurasia, Africa and India (Pocock 1903), and *Atrax* and *Porrhothele* in Australia and New Zealand. In fact, *Macrothele* or a close relative probably reached Australia and New Zealand just prior to the northward rafting of New Zealand in the late Cretaceous (Griffiths 1971). This would require that the Macrothelinae have superior dispersal mechanisms and adaptability than the Hexathelinae. This would account for the wide distribution of *Atrax* in Australia. One of the striking features of *Atrax* associated with its widespread distribution is the small morphological distance between its species. The greater dispersal ability hypothesised for *Atrax* is supported by the fact that there is usually considerable local differentiation in mygalomorphs which have poor dispersal ability (Forster, in Forster and Wilton 1968).

Although *Macrothele* is a widespread genus in Laurasia, such primitive cosmopolitanism does not conflict with the overall hypothesis (Platnick and Nelson 1978). However, the phylogeny of the Macrothelinae requires that *Porrhothele* and *Macrothele* are monophyletic and the biogeographic hypothesis requires that *Atrax* and *Porrhothele* were of most recent ancestry.

The sister group of the ancestor of *Macrothele*, *Porrhothele* and *Atrax*, to which I shall refer as plexathele, strongly resembled *Hexathele* except that the first leg of the male lacked any metatarsal excavation. Plexathele arose in East Antarctica near the Adelaide Geosyncline and was quickly divided into two groups. The vicariance event associated with this was probably the separation of East and West Antarctica by a marginal basin in the late Cretaceous (Craddock 1975).

In the male ancestor of *Hexathele* and *Terania*, a metatarsal excavation appeared. This ancestor was confined to the south eastern edge of Australia and New Zealand, and probably arose just before New Zealand rifted from the Antarctic continent in the late Cretaceous because, in the sister genus of *Hexathele*, the male *Terania* had lost one of the two tibial megaspines, which could not have occurred while New Zealand was still connected to Antarctica.

To the west of Tasmania arose the *Bymainiella*-like ancestral male, which retained at most two tibial megaspines, but that had a broad labium. The range of this group was from southern Queensland southwards, west of Tasmania (because no members of this clade are known from Tasmania or Victoria), through South Australia across Antarctica

into South America. This range was latter fragmented by a barrier (?aridity), thus giving rise to *Bymainiella* in the north, and the ancestor of *Paraembolides* and *Scotinoecus* in the south. The reduction of the anterior lateral spinnerets which diagnoses *Scotinoecus*, occurred subsequent to the rifting of Australia from Antarctica, which was the vicariance event that separated *Paraembolides* and *Scotinoecus*. *Paraembolides* was driven northward by the contraction of mesophytic beech forests in South Australia (Burbidge 1960). Eventually, *Paraembolides* invaded northern New South Wales and Queensland, thus accounting for its close allopatry with *Bymainiella* in these areas.

When a biogeographical hypothesis is constructed a sequence of geological events is proposed to explain the distributions. Because of the lack of specific agreement among geologists of times for the separation of the continents from each other (see Rich 1975) it is difficult to test the biogeographic hypothesis given. However, the separation sequence of the continents which is generally accepted for the theory of sea-floor spreading has been followed here. For Gondwanaland, that is: Africa - India - New Zealand - Australia - South America - all from Antarctica.

It is this sequence of events which prompts the question: Why are there no plesiomorphic hexatheline ancestors in South America, as there are in Australia? At this point, *Mediothele* Raven and Platnick 1978 appears to fill the requirements, but until further phylogenetic analysis indicates otherwise, the position of this genus must remain uncertain.

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COMPARISON OF THREE METHODS FOR ESTIMATING SOLPUGID (ARACHNIDA) POPULATIONS^{1,2}

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ABSTRACT

This 2-year study of solpugids collected at 2-week intervals from Hurley and Lordsburg, New Mexico comparing 12 can traps with 40 trap boards and 40 pieces of natural ground-surface debris demonstrates that can traps are much more reliable in estimating both the mean number of individuals and the number of species in a given area than either of the other two methods tested. Additional methods studies are needed for species not consistently susceptible to can trap collections, and for attaining greater reliability for data on the relative densities of solpugid species.

INTRODUCTION

The present paper presents comparative population data for solpugids obtained during 1974-75 from collections in can traps, under trap boards, and under natural ground-surface debris.

Estimates of solpugid populations have been published by Muma (1963, 1974b, 1975a), Allred and Muma (1971), and Brookhart (1972). The data presented by Muma (1963), Allred and Muma (1971) and Brookhart (1972) were obtained using pit traps (large, dry cans) and were believed by Muma (1974b) to be questionable owing to the ability of solpugids to climb smooth vertical surfaces with their adhesive palpal organs. Some of the data presented by Muma (1974a) are similarly questionable, but that obtained with killing-preserving can traps, used by Muma (1975a), may be statistically valid within relatively broad limits, 30 percent of the mean, as indicated by Muma (1975b). Muma (1974b, 1975b) has inferred that even continuous can trap operation does not produce reliable population data for *Eremochelis bilobatus* (Muma). It is necessary, therefore, to develop and test other methods for estimating solpugid incidence and population density.

The term "population" is used here rather than "abundance" for the following reasons. In North America, solpugids are predominantly nocturnal arachnids. Only 5 or 6

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species are known to be diurnal. Most species are also subterranean, spending the daylight hours and many night time hours in burrows in the soil or under soil-surface debris. At least one species, *Ammotrechella stimpsoni* (Putnam), is known to inhabit termite and wood-boring insect burrows above the soil-surface. Excepting possibly adult males, solpugids do not emerge from their burrows nightly or even regularly. They remain in their burrows for extended periods of time to digest food, to molt, to deposit eggs and to escape extremes of temperature and humidity. Further, some solpugid species are long-legged, run rapidly, and range over large areas. Others are short-legged, with limited ranges. Still others are sedentary, capturing prey by ambush. Most males are longer-legged than females and range widely in search of their more sedentary mates. Therefore, all previous studies and the present study were conducted on the premise that solpugids actively running over the soil-surface or hiding under soil-surface debris are representative of the entire population, either active or inactive, and either subterranean, on the soil-surface or arboreal. As yet, no one has attempted to estimate or compare population sizes of solpugid species per square or cubic meter or per hectare.

METHODS

Muma (1974b) demonstrated that solpugid numbers tend to be larger in the arid grasslands than in the pinyon-juniper life zone of southwestern New Mexico. Therefore, his Hurley and Lordsburg study areas were used for this 2-year investigation in order to assure capture of significant numbers of individuals and species. The topography and plant associations of the 2 areas are described in that publication.

Muma (1975b) demonstrated reliability of the mean number of solpugids collected annually within 30% of the mean in 11 can traps per study area. In this study 12 can traps, those proposed by Muma (1970) and tested by Muma (1975b) were operated in each area. They were 3.79 liter cans with 15.3 cm openings, supported at ground level with a 35 cm square of plywood 6 mm thick, and roofed with a similar piece of plywood on 2 cm legs. These traps were set in 2 intersecting transect lines; 7 oriented north-south at 10 m intervals and 5 oriented east-west at similar intervals. Each trap was provided with 250 cc of a 1:1 mixture of 70% isopropyl alcohol and commercial ethylene glycol. Traps were visited every 2 weeks from 1 April to 1 December of each year, solpugids were screened from the killing-preserving medium and the medium reconstituted with a 3:1 mixture of alcohol-glycol.

Trap boards were planed, pine lumber 4.2 cm thick, 14.3 cm wide and 32.4 cm long. Forty trap boards, arranged in 4 north-south rows of 10 each at 5 m intervals with 5 m between rows, were placed within the arms of the can trap transects in each study area. At each visit, between dawn and 10:00 AM, each trap board was turned over, and any observed solpugids were collected for identification and enumeration.

Natural ground-surface debris consisted of cow dung, yucca logs, and rocks. At each visit, between dawn and 10:00 AM, 40 randomly selected pieces of debris within the arms of the can trap transects were turned over, and any observed solpugids were collected for identification and enumeration.

Early instar immatures, those with 3 pairs of malleoli, were identified only to family. Middle and late instar immatures were identified only to genus. Only adults or easily recognized, and sexed penultimate immatures were identified to species.

Table 1.—Solpugids collected in can traps, under trap boards, and under natural soil-surface debris in 1974 and 1975 at Hurley and Lordsburg, New Mexico.

Solpugids	Years	Hurley			Lordsburg		
		Traps	Boards	Debris	Traps	Boards	Debris
Eremobatidae (Juv)	1974				10		
	1975				10		
<i>Eremorhax</i> (yg)	1974				1		
	1975				3		
<i>Eremorhax</i> species #1	1974	1			2		
	1975				1		
<i>Eremobates</i> (yg)	1974	59	5	4	32	5	2
	1975	14	1		60	14	7
<i>Eremobates</i> species #1	1974	1			12		
	1975				14		
<i>Eremobates</i> species #2	1974	5			17		
	1975	2			24		
<i>Eremobates hessei</i> (Roewer)	1974	5			8		
	1975				16		
<i>Eremobates</i> species #3	1974	11			8	1	
	1975	5			9	4	
<i>Eremochelis</i> (yg)	1974						
	1975				1		
<i>Eremochelis bilobatus</i> (Muma)	1974				1		
	1975				1		1
Ammotrechidae (Juv)	1974						
	1975						
<i>Ammotrechula</i> (yg)	1974						
	1975						
<i>Ammotrechula peninsulana</i> (Banks)	1974				1		
	1975				1	1	
<hr/>							
Sub-Totals	1974	82	5	4	92	6	2
	1975	21	1		140	19	8
Totals		103	6	4	232	25	10

RESULTS

Table 1 presents the accumulated data summarized on plot, annual, and total bases.

Seasonal data, not tabulated, showed that the can traps-captured about 10 times the total number of solpugids taken each season by either or both of the other 2 methods. However, in the spring of 1975 at Lordsburg only 5 times as many were taken in the can traps.

DISCUSSION

It is not necessary to apply statistical analyses to the data in Table 1 to determine that can traps, as used, collected a far larger sample of solpugid specimens and species than either or both of the other 2 methods, as tested. In fact, the data indicate that estimation

of solpugid populations by turning over natural or artificial ground-surface debris and counting or collecting the specimens would be highly erroneous unless either much larger or much more frequent samples were utilized. Two species were not taken under either natural or artificial ground-surface debris, and no juveniles were collected by either method. Further, since Muma (1975b) has demonstrated stability of the mean number of solpugids collected with 11 can traps at a site, within 30% of the mean, it can be assumed that *Eremobates* species #2 was more common at the Lordsburg plot than *Eremobates* species #3, but the trap board data indicate just the reverse. Using the same logic, *Eremobates* sp. #3 was more common at the Hurley plot than *Eremobates* sp. #2, but neither of the species was collected under natural or artificial ground-surface debris at that plot. The utilized number of can traps per plot was, therefore, much more reliable for estimating solpugid incidence and population density than searching under natural or artificial ground-surface debris. It should be emphasized, however, that although can traps have been validated within broad parameters for solpugid studies, searching under artificial or natural ground-surface debris has not been examined statistically. Furthermore, can traps are continuous sampling devices and to be numerically comparable, the turning over of ground-surface debris would have to include a greater number of pieces of debris or much more frequent sampling, as stated above. The present study merely indicates that beyond the setting of can traps and the placing of trap boards, can traps produce more reliable data per time expended than trap boards or natural ground-surface debris.

The collection data presented here for *Eremochelis bilobatus* (Muma) confirm the inference of Muma (1974b, 1975b), that can traps do not produce reliable data for this species. The same also may be true for *Eremorhax* species #1 and *Ammotrechula peninsulana* (Banks).

Additional methods of research studies are needed for more reliable estimation of both solpugid incidence and solpugid population density.

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PITFALLS IN SPIDER COMMUNITY STUDIES (ARACHNIDA, ARANEAE)

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ABSTRACT

Pitfall traps of four types were used at three woodland sites over twelve months in an empirical study of the effect of trap efficiency in describing species composition of spider communities. There was a certain degree of agreement between trap-types in terms of seasonal variations and relative numbers of species and of individuals at the three sites.

Due to the different responses of the various species, distortions were evident in the communities' species frequency curves. This was significantly apparent at one of the sites and less so at the others. The more "efficient" methods used here captured disproportionately more species in relation to the greater number of individuals. The probability of analogous distortions in data from other sampling methods is discussed.

THE PROBLEM

Pitfall traps are commonly utilised by arachnologists, although the validity of their use is questioned by some. Uetz and Unzicker (1976) compare pitfalls with quadrat sampling and give qualified support for the former method in studies of cursorial spiders; they quote further references both for and against the technique. Other considerations may be found in Turnbull (1973) and Duffey (1972). It is generally appreciated that the capture rate in pitfalls depends on both population density and on activity, e.g. Vlijm and Kessler-Geschiere (1967). Trap efficiency is also important and may vary between species and between habitats, as considered by Maelfait and Baert (1973) for arachnids, and for beetles by Baars (1979) whose field experiments and computer simulations indicated that continuous pitfall sampling gave reliable relative measures of carabid populations. A thorough study of pitfall trap efficiency in capturing Coleoptera has been made by Luff (1975).

While there have been criticisms of the accuracy of the method, there has been no explicit consideration of the way in which trapping efficiency may distort information on the relative importance (a function of both density and activity) of species in a community. Based on data from an empirical study, it is with this aspect that this paper is concerned, concentrating on community parameters rather than individual species.

METHODS

To address the question - "Do traps of different efficiency give the same representation of species composition in a community?" - pitfall trap efficiency was varied by using four types of trap:

1. Control—plain plastic jar, 6 cm diameter, 8 cm deep, with drainage holes bored at intervals 1.5 cm below rim.

2. Detergent—as type 1 but with 1-2% solution of the detergent teepol to a depth of 1-2 cm.

3. Detergent + preservative/killing fluid—as type 2 but incorporating 4% formalin solution.

4. Dry—as type 1 but with a horizontal, opaque cover placed over the trap to prevent entry of rain-water and with 2 cm clearance below the cover to allow access for invertebrates active on the soil surface.

To allow for any environmental gradients, the traps were placed in a 4 x 4 Latin square with a pair of similar traps in each 1 m² cell. The study commenced in October 1976 and for the initial three months three pairs of traps were placed in each cell and trapping periods of 1, 2 and 4 weeks employed. Analysis of variance applied to each of these sampling periods showed that trap type affected the number of animals caught; trap location in the sampling grid was not correlated with animals captured (Stewart 1977). After this initial experiment, traps were lifted each month. Data obtained over a full year are considered here.

The experiment was carried out in the Loch Lomond National Nature Reserve, Scotland, at three contrasting sites which provide araneid/opilionid communities of different types (Curtis et al. 1978):

Site 1—Oak-dominated deciduous woodland on island of Inchcailloch; ground vegetation includes various grasses, bramble (*Rubus fruticosus* agg.), woodrush (*Luzula sylvatica*) and ferns such as bracken (*Pteridium aquilinum*) and *Dryopteris* spp.

Site 2—Mixed deciduous woodland on mainland, about 4 km from site 1, with fairly similar ground flora including rather more abundant mosses, but with land links to contrasting habitats.

Site 3—Wet birch (*Betula pubescens*) woodland on mainland, only 150 m from site 2, but with markedly different ground flora comprising mainly mosses: *Sphagnum* and *Polytrichum* spp.

RESULTS - DATA AND DISTORTIONS

About 11,000 individuals, representing 130 species, were collected. At all three sites, trap types 2 and 3 were clearly most "efficient," capturing more individuals and more species than types 1 and 4. This can be seen in Table 1, which also gives data for some of the more numerous species. While many species follow the overall trend in trap efficiency, there are important variations. A notable exception is the most abundant species, *Nemastoma bimaculatum* (Fab.), which was captured most in type 1 traps and least in type 2.

Seasonal variations.—In spite of their different capture rates, the four trap types showed similar seasonal variations of abundance typical in temperate woodland spider communities. This applies to numerical abundance and species richness and is illustrated in Fig. 1. All three sites show an increase in numbers from February. This appears as a peak at sites 2 and 3. At sites 1 and 2 linyphiid species such as *Diplocephalus picinus* (Blackwall) and *Lepthyphantes tenebricola* (Wider) contribute to this spring/early summer peak especially evident in type 2 traps. The lycosid, *Pirata hygrophilus* Thorell is another contributor to the site 2 peak and is involved at site 3 where other lycosids are also prominent together with the linyphiids *Cnephalocotes obscurus* (Blackwall) and

Table 2.—Correlations between the patterns of monthly changes in (a) species richness and (b) abundance, shown by the four trap types; expressed as Spearman's rank correlation coefficient with significant ($p < 0.01$) values underlined.

(a) SPECIES RICHNESS											
Sites:	1			2			3				
Trap types	1	2	3	1	2	3	1	2	3		
4	.51	<u>.79</u>	.68	4	.46	.43	.52	4	<u>.75</u>	<u>.82</u>	<u>.77</u>
3	.69	<u>.90</u>		3	<u>.71</u>	<u>.86</u>		3	<u>.74</u>	<u>.88</u>	
2	<u>.76</u>			2	<u>.70</u>			2	<u>.79</u>		
(b) ABUNDANCE											
Sites:	1			2			3				
Trap types	1	2	3	1	2	3	1	2	3		
4	<u>.70</u>	.61	.62	4	<u>.72</u>	.19	.35	4	<u>.87</u>	<u>.81</u>	<u>.95</u>
3	<u>.84</u>	<u>.87</u>		3	<u>.72</u>	.60		3	<u>.83</u>	<u>.92</u>	
2	<u>.78</u>			2	.54			2	<u>.72</u>		

Tapinocyba pallens (O.P.-Cambridge). At site 1 the abundance of harvestmen is responsible for the gradual increase in numbers through the year to a peak in September/October. A peak in species richness is evident at each site around May/June and a smaller peak in October/November.

Inspection of Fig. 1 shows differences between the different trap-types, which depend on their relative efficiencies for particular species. Note especially the high capture totals for type 1 traps at site 1 towards the end of the sampling period. This is due to the greater importance of *N. bimaculatum* at this site relative to sites 2 and 3. Nonetheless, there is a good deal of agreement between the trap types in terms of the relative numbers of individuals and of species recorded each month. Rank correlation coefficient values comparing the patterns of monthly variations are given in Table 2. Considering as significant values for which $p < 0.01$, all four types of trap agree with each other at site 3. More disagreement is evident at sites 1 and 2 with their greater proportion of opilionids, especially at site 2 with strong agreement only of type 1 with type 3 and with type 4.

Community structure.—To examine this aspect, the data were considered in terms of four quarterly periods: Q1 - October, November, December; Q2 - January, February, March; Q3 - April, May, June; Q4 - July, August, September. This approach avoids the problems of small sample size for single months but still gives an indication of variations over the year. Species frequency distributions are used here, plotting $S(n)$ - the number of species represented by n individuals - versus n on a logarithmic (to the base 2) scale. This is just one of several alternative ways of presenting species abundance relationships (May 1975) and serves well to illustrate the distortions present in these pitfall trap results.

Species frequency distributions for the three sites in each quarter are illustrated in Fig. 2. Comparison of the three sites in any one period shows differences between the curves

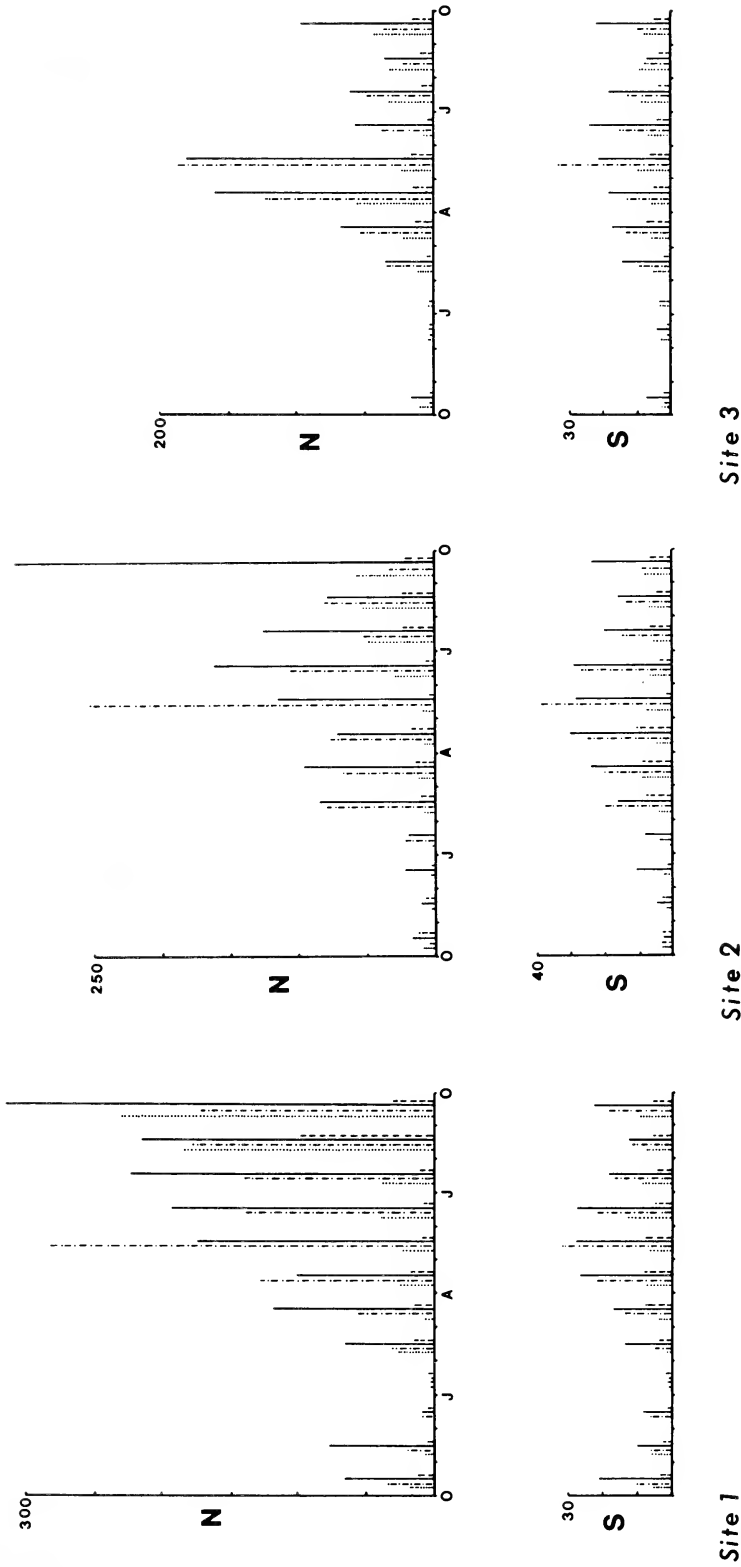


Fig. 1.—Variations in number of individuals (N) and of species (S) taken in each month. Four bars are drawn in each month referring to the four types of trap: dotted line - type 1, dots/dashes - 2, solid line - 3, broken line - 4. The months marked (O - October, J - January, A - April, J - July) indicate the start of the quarterly periods considered.

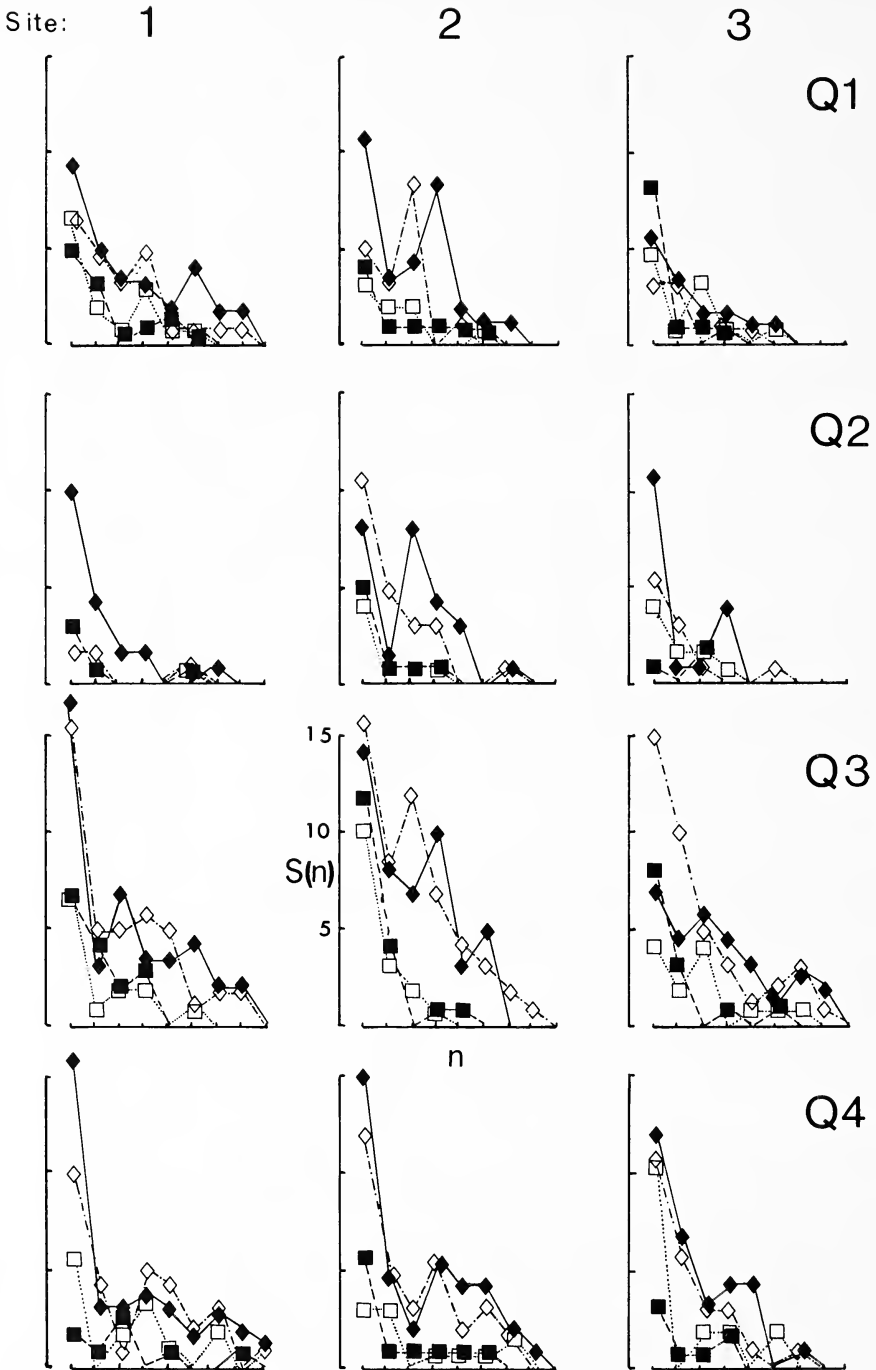


Fig. 2.—Species frequency diagrams showing $S(n)$ = number of species represented by n individuals plotted against n with the n axis in terms of octaves, i.e. 1, 2, 4, 8, 16, 32, 64, 128 and 256: $S(4)$ = no. of species with capture total of 3-4 individuals, $S(8)$ with 5-8, etc. Note differences in the shape of these curves between sites and between quarterly periods. In particular, observe differences between trap-types at site 2, where clear separation between the curves is evident for moderately abundant species, especially in Quarter 3. Open squares represent trap-type 1, open diamonds - 2, solid diamonds - 3, solid squares - 4.

from the sites, presumably reflecting different community structures at the sites. Also, at each site the shape of the species frequency plot changes from one period to another. At sites 1 and 3 the curves from the different types of trap are similar, but there are noticeable variations at site 2. Here, trap types 2 and 3 strongly increase the frequency of moderately abundant species, a phenomenon which is most clearly evident in Q3, but also present at other times of the year.

Fig. 3 shows species frequency plots for data amalgamated over the full year and emphasises the different distortions evident at the different sites. At sites 1 and 3 there is no significant difference between distributions from different trap types, but at site 2 trap types significantly altered the frequency distribution ($\chi^2 = 40.1$, d.f. = 12, $p < 0.001$). This clearly has implications for data interpretation.

Number of species recorded (S) is plotted against number of individuals (N) for each trap-type at each site in Fig. 4. The usual curvilinear relationship is apparent but there is also clear separation of trap-types 2 and 3 from 1 and 4. This was also seen in data from each quarter, with a most noticeable separation of types 2 and 3 from 1 and 4 occurring in Q3.

DISCUSSION AND CONCLUSIONS

A reassuring feature of Fig. 4 is that the data points for the more "efficient" trap-types 2 and 3 lie about the asymptote of the curve. This suggests that best representation of species richness would be achieved by using these types of trap (preferably type 3, in which the preservative keeps specimens in better condition).

Use of a rarefaction technique (Heck, van Belle and Simberloff 1975) to calculate $E(S)$, estimated species richness for a standard sample size, is an effective way of describing species diversity. A general trend apparent in each quarterly period was for trap types 2 and 3 to yield higher $E(S)$ values than 1 and 4. This is demonstrated in Fig. 5 which shows $E(S)$ values for a standard sample size of 100 adults, using the full year's data. The higher $E(S)$ values at site 2 accord with the noted distortion in species frequency distribution, but this marked pattern in $E(S)$ is also shown at sites 1 and 3. Clearly the use of traps of different efficiency will give different impressions of species richness in a com-

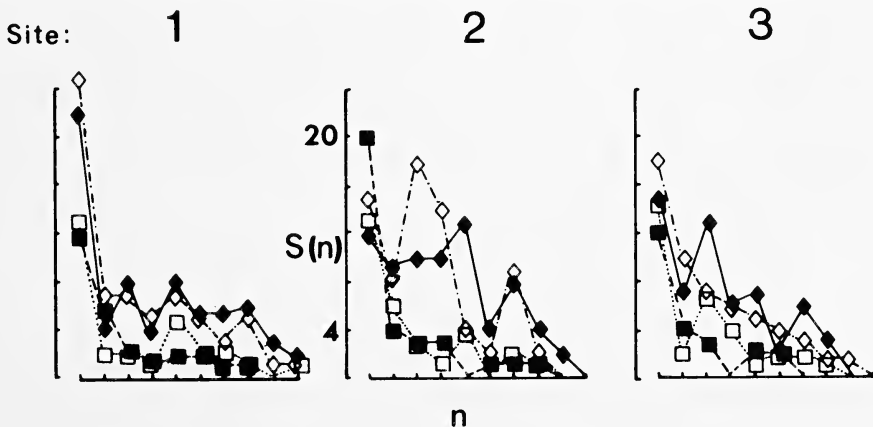


Fig. 3.—Species frequency diagram for three sites' data over whole year. Symbols as Fig. 2. Again the most obvious variations with trap-type may be seen at site 2 with the deviation of types 1 and 4 (squares) from types 2 and 3 (diamonds).

munity. Fig. 5 indicates that in the more "efficient" traps the increase in S is *not* a direct consequence of increase in N .

As considered by Uetz and Unzicker (1976), N may be increased by increasing the number of traps, or trap density. Unpublished data from an experiment carried out in October 1977 show this. A 5 x 5 Latin square of 1 m² quadrats was used. Trap densities of 1, 2, 4, 8 and 16 per square metre over this area showed that mean number of captures per trap was not affected by trap density. Curtis (1978) used 20 plain pitfalls within 1 m² quadrats to increase sample size. However, this dodges the question - Does the species abundance pattern in pitfall samples reflect the pattern in the community being sampled? Obviously at site 2 the disagreement between trap-types indicates that at least some types do not give an accurate picture of the field situation. Even at the other sites, where there is agreement between the types of trap, one cannot be certain that the species frequency distribution recorded in the pitfall samples also applies to the community under study.

It is well appreciated that pitfall trap capture rate depends on (e_{ih} , a_{ih} , d_{ih}), where e_{ih} = trapping efficiency, a_{ih} = species' activity and d_{ih} = species' density, for species i in habitat h . Variations in these parameters cause distortions and have implications for the use of many ecological approaches based on species' relative abundances. Examples include the Shannon (1948) diversity measure as used by Uetz (1975, 1976), Levins' (1968) formulation for niche breadth (Uetz 1977), its corollary as a measure of species diversity and Hurlbert's (1971) probability of interspecific encounter used by Curtis (1978), as well as the index of overlap used by both of these authors.

A traumatic development is to re-define e_{ih} as the efficiency of any other method of sampling. Just as e_{ih} applied to a pitfall reflects the probability that a spider having fallen into the trap cannot escape, it could also be taken to represent the probability of retention in a sampler's hand, or of separation in a thermal extraction apparatus. Just as the likelihood of a spider falling into a pitfall trap depends on its activity, a_{ih} , the probability of its capture by hand is greatly increased by its activity rendering the specimen more noticeable to the searcher; a physiologically inactive individual will not respond to the temperature/humidity gradient in an extraction apparatus such as a Berlese or Tullgren funnel. So the types of distortion described explicitly in this paper are also applicable to the other sampling methods employed by ecological arachnologists.

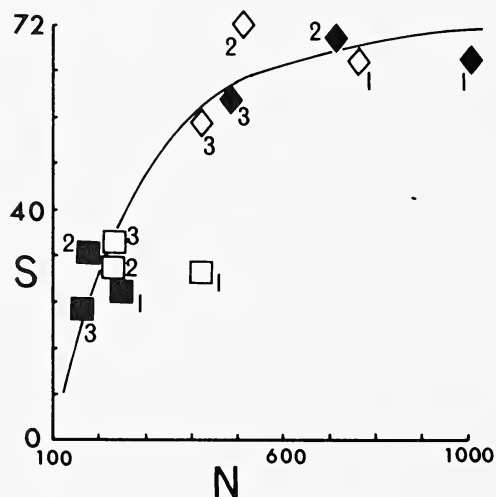


Fig. 4.—Plot of number of species (S) versus number of individuals (N) captured over the year in the four trap-types (symbols as in Fig. 2) at the three sites (site numbers beside symbols). Clear separation of types 2 and 3 (diamonds) from 1 and 4 (squares) is obvious. Curve is fitted by eye.

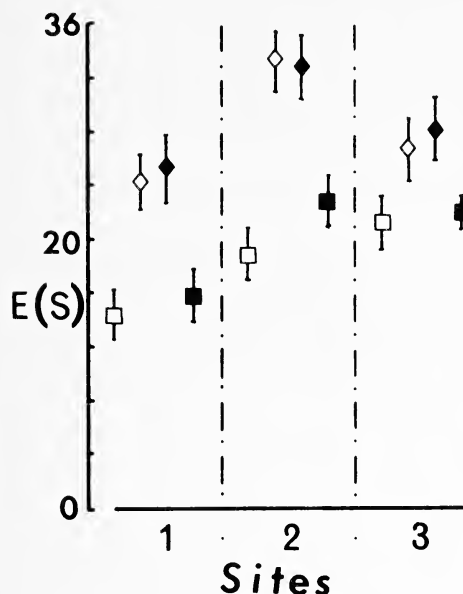


Fig. 5.—Values of $E(S)$ - estimated number of species for a standard sample size of 100 adults. Based on full year's data. Symbols relate to trap-types as in Fig. 2 and the bar extends one standard deviation above and below symbol. Markedly higher values are evident for trap-types 2 and 3 (open and closed diamond symbols).

Perhaps the high numbers of species recorded in pitfall traps, coupled with the continuous nature of their sampling, argue in favour of their use. In any case, although great caution is required in attempting to describe spider communities, the hypotheses generated in these studies are useful from a heuristic point of view.

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RESEARCH NOTES

AN UNUSUAL DEVELOPMENTAL ANOMALY IN SCORPIONS (SCORPIONES, BUTHIDAE)

Developmental anomalies, including duplication of body parts, are known to occur in two families of scorpions. In the family Chactidae, Pavesi (1881) reported a specimen of *Euscorpius germanus* (C. L. Koch) with distal symmetrical duplication of the body starting from mesosomal segment IV.

Most reports of body duplication, however, are for members of the family Buthidae. Shulov and Amitai (1955), reported on a specimen of *Leiurus quinquestriatus* H. et E. with two stingers. A similar case was reported by the author in *Tityus serrulatus* Lutz e Mello (Matthiesen, 1978). Vachon (1972) illustrated an adult *Isometrus maculatus* (Geer) with partial duplication of the venom vesicle, and a short, partly atrophied second stinger. Williams (1971) described an adult *Centruroides sculpturatus* Ewing with two fully formed, functional telsons. Distal duplication of the metasoma from segment II is reported by Berland (1913) for *Centruroides infamatus* (C. L. Koch); and from segment I for *Centruroides noxius* Hoffman by Briseño (1963), for *Centruroides margaritatus* (Gervais) by Campos (1918), for *Androctonus crassicauda* (Oliver) by Millot and Vachon (1949), Vachon (1952, 1953), for *Centruroides sculpturatus* Ewing by Williams (1971), and for *Buthotus alticola* (Pocock) by Vachon and Serfaty (1950). Distal duplication



Fig. 1.—Embryo of *Tityus cambridgei* Pocock, with duplication of anterior body parts.

starting on mesosomal segment IV has been reported for *Buthacus leptochelys* H. et E. by Sergent (1946) and Vachon (1952), and duplication from mesosomal segment III in *Centruroides gracilis* (Latreille) by Franganillo (1937 apud de Armas, 1977).

Duplication of the anterior region of the body is not as common as duplication of the posterior region. Brauer (1917) reported several embryos of *Euscorpius carpathicus* L. in which he observed duplicated prosomas, including on some duplication of some of the anterior segments of the mesosoma.

In Brazilian species of the genus *Tityus* Koch (Buthidae), I observed many cases of teratological embryos of different kinds (Matthiesen 1970). The one described below represents the first known case of duplication of anterior body parts in buthids. The embryo (Fig. 1) was found in a female *Tityus cambridgei* Pocock from Belem, State of Para, Brazil (26 May 1967), collected and dissected by Prof. Maria M. Telles. It's anterior end is clearly double, showing two carapaces each with a complete set of eyes, and four pedipalps. The embryo is asymmetrical, with the right side being smaller than the left one. The single metasoma, which in normal embryos is folded ventrally, in this case is folded dorsally, obscuring the location where the two anterior halves come together.

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PERSISTENT STICKINESS OF CRIBELLUM SILK

Capture threads made by cribellate spiders are covered with balls of a sticky, viscous liquid which gradually dries out (e.g. Kullmann 1975) and loses most of its stickiness. Cribellate spiders' sticky thread is very different, being composed of a cloud of very fine threads about $0.015\ \mu$ in diameter (Lehmensick and Kullmann 1957, Friedrich and Langer 1969). The degree of "wetness" of cribellate silk is not clear. Many authors (e.g. Comstock 1940: 192, Gertsch 1949: 137-138, Bristowe 1958: 79, Kaestner 1968: 171, and Forster and Forster 1973: 209) have used the word "viscid" to describe it, intentionally or unintentionally implying that it is wet ("viscid" is defined in Webster's New World Dictionary of the English Language as "thick, sirupy, and sticky; viscous"). Kullmann (1975: 325) on the other hand describes it as dry, but offers no evidence. This note describes an observation which shows that cribellate sticky silk is probably dry, as it does not lose its stickiness on prolonged exposure to dry conditions.

A wooden frame in which a mature female *Uloborus diversus* (Uloboridae) had built an orb was placed in a small laboratory oven turned to "low," and left there for three months during the winter in Cambridge, Mass., where indoor humidity is low (usually 10-20%). At the end of this time, it was removed and immediately tested. When the tip of a lead pencil was touched to individual stands of sticky spiral, the silk stuck readily; there was no obvious difference compared to new silk.

As noted and clearly illustrated by Kullmann (1975: 325), the stickiness of cribellum threads is not simply due to the fine fibers becoming entangled in substrate irregularities as is sometimes stated (e.g. Kaestner 1968: 171). Its persistent stickiness implies that it is superior to "wet" sticky silk. In nature, however, the stickiness of cribellum silk is often substantially reduced within a few days or less due to rain or dust accumulation.

I thank W. J. Gertsch for identifying the spider. The observations were made in the office of H. W. Levi while I was a graduate student at Harvard University.

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LEIOBUNUM TRIMACULATUM GOODNIGHT AND GOODNIGHT
IS A SYNONYM OF *L. BIMACULATUM* BANKS
(OPILIONES, LEIOBUNIDAE)

In 1893, Nathan Banks (Canadian Ent. 25: 210) described a striking new species of *Leiobunum* from specimens in the collection of Dr. George Marx. The pairs of brilliant yellowish-white spots on the dark brown to black body provided the obvious name of *bimaculatum*. According to Banks, the specimen came from "southern California." Later, Crosby and Bishop (1924. J. Elisha Mitchell Sci. Soc. 40: 16-18) redescribed numerous specimens from the Gulf Coast of the eastern states, remarking on a fact that had by then become quite obvious: George Marx's locality labels were totally unreliable. Crosby and Bishop examined what they called the male lectotype, an unlabelled specimen in the Museum of Comparative Zoology (MCZ), and doubted that the original material came from California at all, since the species had never been recollected there (and has not been as yet, some 86 years after the publication of the original description). Davis (1934. Amer. Midl. Nat. 15: 669-670), in a revision of *Leiobunum*, listed only southeastern United States records for *bimaculatum*, and refers to a male type. Goodnight and Goodnight (1943. Amer. Midl. Nat. 29: 650-651) thought it necessary to provide a new name, *L. trimaculatum*, for material of *bimaculatum* from Florida. They did not mention the possibility that Banks' original attribution of the type locality might have been in error, but did refer to Crosby and Bishop's 1924 account. Goodnight and Goodnight found differences between their *trimaculatum* types from Ocala, Florida, and Banks' *bimaculatum* type specimen (again, said to be a male). They referred to "a somewhat different arrangement" of the dorsal spots, and averred that when "... *L. bimaculatum* and *L. trimaculatum* are seen side by side, they are quite distinct." There also appeared to be slight size differences.

In examining material of various species of *Leiobunum* in order to determine the true extent of the genus, I had the opportunity to study the type specimens of *bimaculatum* and *trimaculatum*, as well as a considerable number of specimens from the Florida State Collection of Arthropods. I could find no distinctions among these specimens, types and otherwise, that would suggest two species are involved.

There are two specimens of *L. bimaculatum* in the type collection of the Museum of Comparative Zoology. One of these, which we may suppose is the original Marx specimen, is a female labelled "type" in Nathan Banks' distinctive handwriting, but has no locality label. The second specimen, a male, is labelled, also by Banks, as having been collected by Davis in Gainesville, Florida; it is not labelled as a type. In neither case had the genitalia been dissected. In the card file on arachnid types, there are likewise two cards. One of these gives the locality as "North America," the other as "Gainesville, Florida." Both cards are clearly marked "type." It is well known that Nathan Banks had the habit of adding additional specimens to type vials, or even substituting newly collected specimens he considered as better examples of the species. In this case it is likely he simply added a vial to the collection. Davis (1934) lists no specimens collected by himself from Gainesville (though he does list Alachua County records), so the addition probably was made in the early 1930s or later. I compared measurements of the leg femora of each of the MCZ specimens with those given by Banks (1893) and by Goodnight and Goodnight (1943). The results did not fully agree in either case, and allowed no conclusion to

be drawn, but I suspect that Davis saw the Marx female, and that Goodnight and Goodnight also examined it, since Davis does not give a type locality (the Marx specimen is unlabelled) and Goodnight and Goodnight persist in using the data published by Banks with the original description. The Gainesville specimen in the MCZ type collection is clearly labelled as to locality, but is not labelled as a type.

Because a specimen (the Marx female) designated as a type by the original author still exists, the use of the term "lectotype" by Crosby and Bishop (1924) was not justified, nor would the designation of the Gainesville male as such be appropriate now. But in the absence of a clearly correct locality for the holotype specimen, it would be best to consider the Gainesville male as a paratype selected later by Banks and to restrict the type locality to Gainesville, Florida.

Since nothing resembling *bimaculatum* has been recollected in California, and I can see no significant differences in the specimens I studied, I believe that Goodnight and Goodnight were in error when they described "trimaculatum" as new, and I relegate that name to the synonymy of *L. bimaculatum*. *Leiobunum bimaculatum* is common along the Gulf and Atlantic coastal plain, from Biloxi, Mississippi, to the South Carolina/North Carolina border, with an isolated record from Virginia Beach, Virginia.

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THE JOURNAL OF ARACHNOLOGY

Instructions to Authors

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Manuscripts are acceptable in English, French, Portuguese, and Spanish, and must be typed double or triple spaced throughout. Use good bond paper 8.5 by 11 in. in size, but not erasable bond. Leave ample margins, at least 1.5 in. on the left, and do not hyphenate any words at the right margin. To facilitate prompt review by two or more referees, send the Editor the original manuscript and two carbon or good xerox copies, together with copies of the illustrations, for mailing to referees. Follow the recommendations of *Council of Biological Editors (CBE) Style Manual*, unless indicated otherwise below. Do not edit your own manuscript: *italics* are permitted only to indicate scientific names; only the TITLE, PRIMARY HEADINGS (e. g. INTRODUCTION, etc.), and RUNNING HEAD should be typed in capital letters.

Manuscripts longer than about 1500 words (five double-spaced typewritten pages in Elite, six double-spaced typewritten pages in Pica) should be prepared as Feature Articles, shorter papers as Research Notes.

Manuscripts and all related correspondence must be sent to Dr. B. J. Kaston, Associate Editor, 5484 Hewlett Drive, San Diego, California 92115, U.S.A.

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Arrange the various parts of feature articles in the following sequence: (1) mailing address, (2) title, (3) by-line, (4) body of text, (5) acknowledgments, (6) literature cited, (7) figure legends, (8) abstract, (9) footnotes, (10) running head, (11) tables with legends, (12) figures. Put only numbers 1, 2 and 3 above on page 1, and start page 2 with number 4 above, numbering all other pages consecutively.

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4 3

The following special directions apply to authors of taxonomic papers:
(a). Do not use abbreviations to indicate that a new name or a new combination is being proposed in a primary heading (e. g., *A-us x-us*, new species, rather than *A-us x-us*, n. sp. or comparable abbreviations).

(b). Keys must be typed following the third example given in the *CBE Style Manual* (3rd ed., p. 66), which is as follows:

- 1. Use Arabic numerals to designate the leading entry of a couplet2
Do not designate the second entry of a couplet, either by means of numbers, letters, or other marks 3
- 2. Type numbers flush to left margin, and start entry on third space. The second, and subsequent, lines of one entry must be indented five spacesSTOP

(c). Synonymies must follow the abbreviated style shown below:

A-us x-us Jones 1930:3, 1935:9; Russell 1945:453; Smith 1954a:16, 1954b:678; Cooper and Lim 1955:18 (in part).

A-us y-us Bates 1932:18, fig. 4. NEW SYNONYMY.

A-us z-us: Miranda 1948:98 (misidentification); Harris 1951:3 (in part ?). (*nec A-us z-us* Zimmer

(d). Lists of specimens examined of a given taxon must be the last item typed in the treatment of that taxon as they will be set in smaller type. Adhere to the following style for listing specimens examined: Country: state or comparable political subdivision; county or district, detailed locality (elevation), 14 July 1945 (collector), 2 males, 5 females (acronym of institution where specimens are deposited), next detailed locality within that county, and so forth; next county in the same state; and so forth: next state in the same country: and so forth. Next country: and so forth. Punctuation rules are very simple. Use a period to separate countries, colon to separate states, semi-colon to separate counties, and commas to separate specific localities.

Acknowledgments.—Avoid overlooking persons who have in some substantial way assisted with the work. Authors of taxonomic papers should spell out the name, and indicate parenthetically the acronym, of institutions where specimens studied are deposited.

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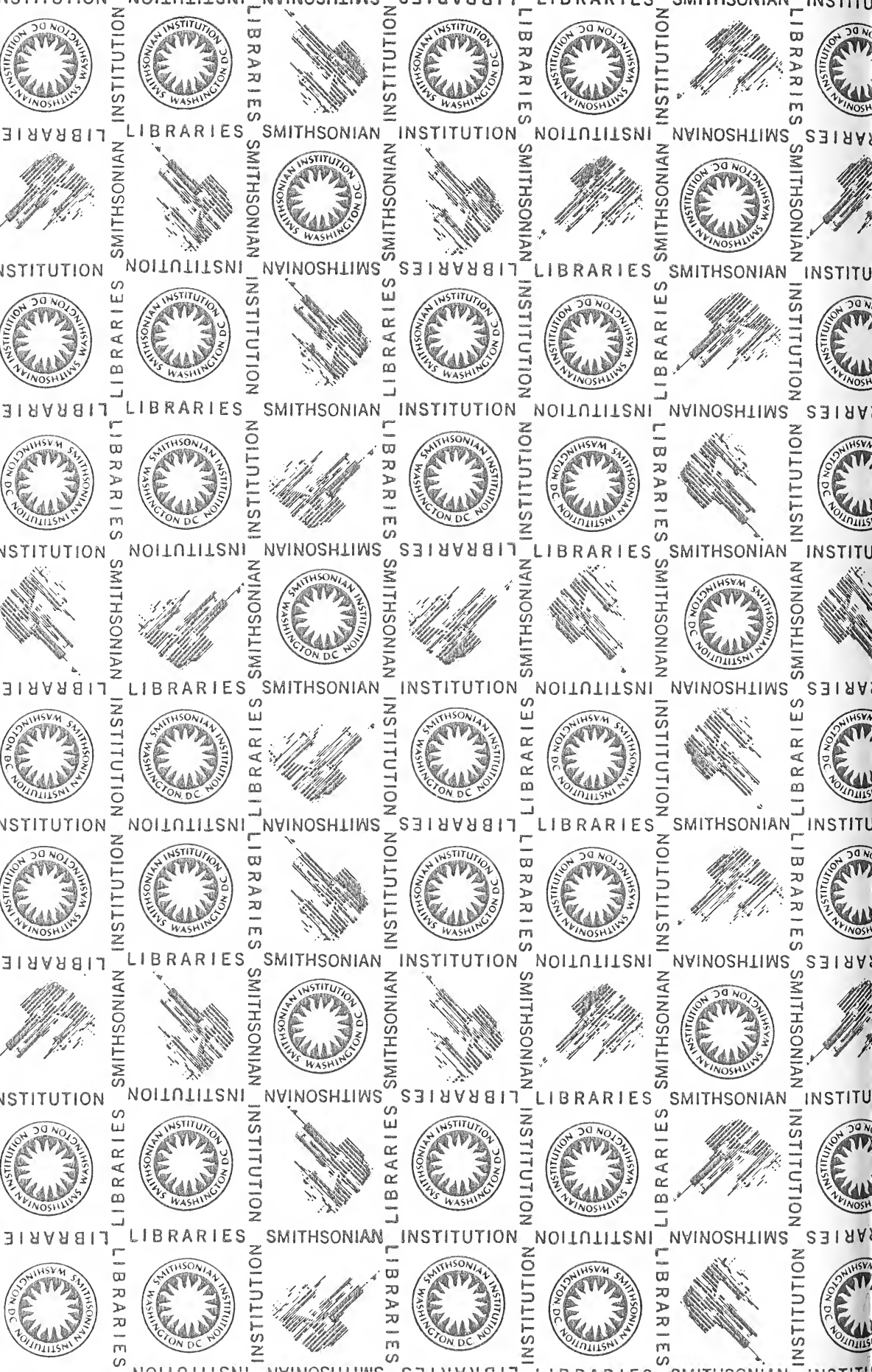
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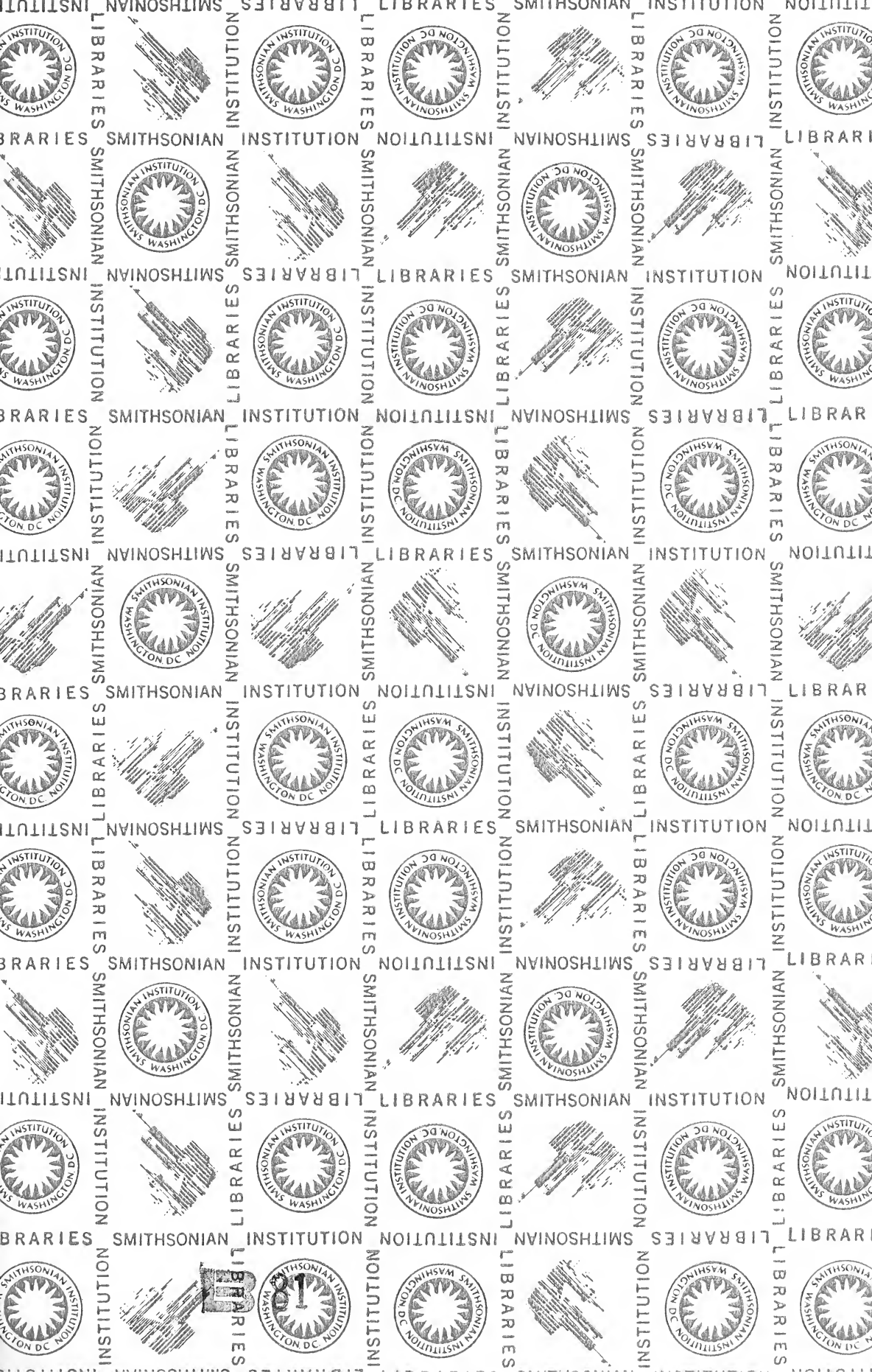
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